ECOLOGY, BEHAVIOUR AND POPULATION DYNAMICS OF THE HARTMANN ZEBRA *EQUUS ZEBRA HARTMANNAE* MATSCHIE, 1898 IN SOUTH WEST AFRICA.

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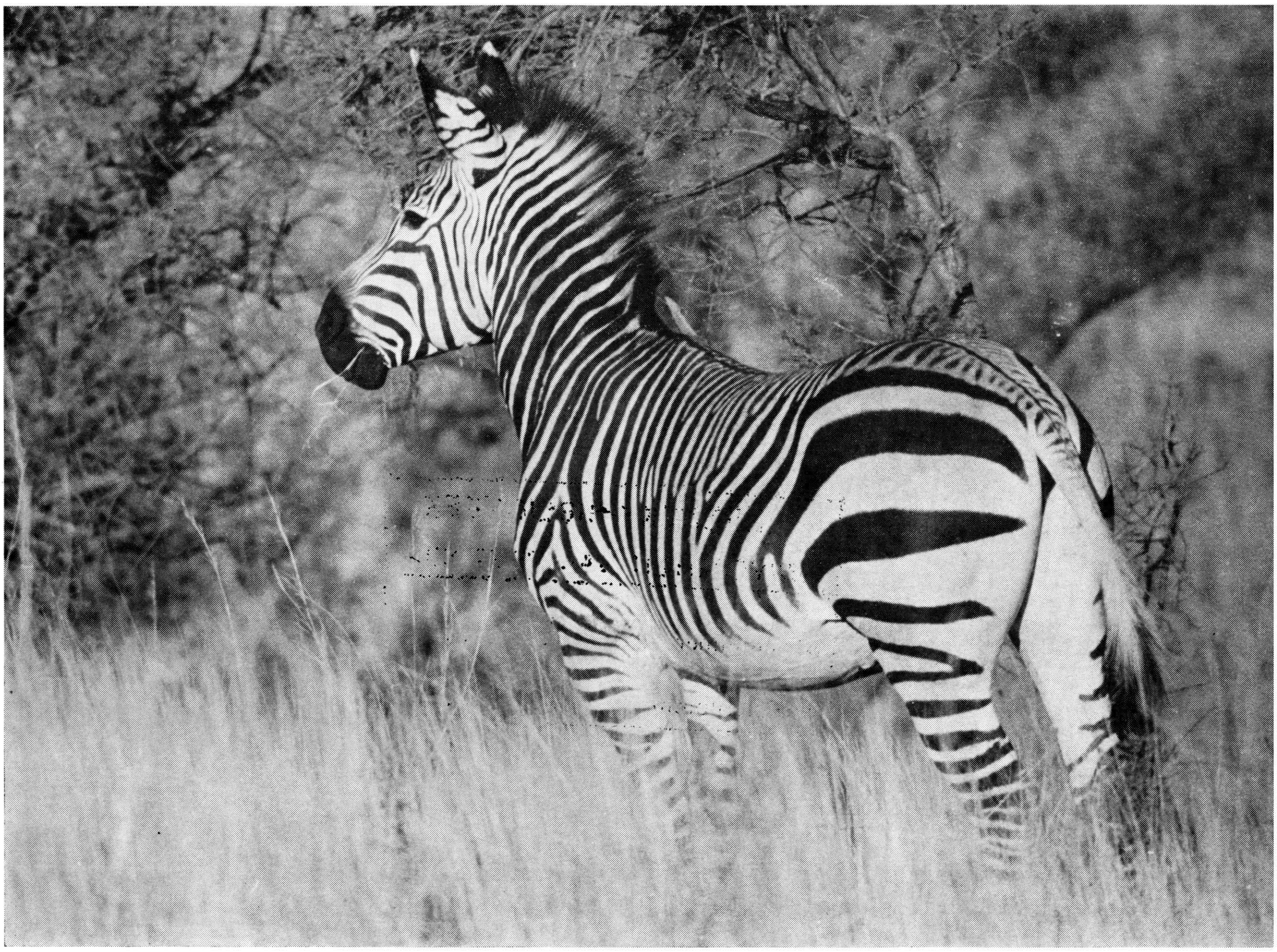

Plate 1: Hartmann zebra (*Equus zebra hartmannae*) in a typical alert stance.

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INTRODUCTION.

The research projects undertaken by the Nature Conservation and Tourism Division of the South West Africa Administration are scheduled according to certain priorities. These priorities are determined by the Director in consultation with his research staff. Projects on the ecology and behaviour of endangered species head the list. This is normally followed by translocation of these species to areas where their survival may be ensured. Animals which, owing to their habits or life requirements, come into competition with man and his livestock, aptly named 'problem animals', also rate a high priority. With the Hartmann zebra, Equus zebra hartmannae, the problem arises that it is both an endangered species as well as a 'problem animal'.

The Hartmann zebra occur for the greater part of their distribution on the mountainous zone along the Namib desert. This area is extremely marginal. They still occur in reasonable numbers and during drought years especially, present serious competition to livestock for grazing. Stampeding herds of Hartmann zebra occasionally cause damage to fences. Although Hartmann zebra are declared Specially Protected Game and no hunting without permits is allowed, it was found that they were being illegally exterminated at an alarming rate. Furthermore, with the implementation of the Odendaal Commission's proposals, it so happened that the Hartmann zebra as a species was not properly protected in any of the existing game reserves. This was mainly due to the lack of suitable habitat in the game reserves.

The Administration of South West Africa, bought a farm in the Naukluft mountains. This farm is situated in typical Hartmann zebra habitat and was proclaimed as a game reserve especially for Hartmann zebra. It is, however, comparatively small, does not conform to certain ecological principles, and would not have supported a representative sample of Hartmann zebra. At approximately the same time the whole area was in the grip of a very severe drought and because of mounting pressure by farmers,something had be done about the Hartmann zebra problem. It was decided by the Director that a research project should be launched to determine the status, distribution, ecology, behaviour and population dynamics of the Hartmann zebra. The results of this project will enable the Administration of South West Africa to formulate a policy that will ensure the survival of a representative sample of the Hartmann zebra population in South West Africa and also satisfy the farming community.

TAXONOMY AND DISTRIBUTION OF THE LIVING AFRICAN EQUIDAE.

In Africa the Equidae are represented by asses and zebras. The zebras are characterized basically by the dark and lighter coloured bands over the body. A considerable individual variation in the appearance of these bands occurs, especially in the Burchell zebra. This resulted in a host of names being given to various localized groups, causing considerable confusion. Several major revisions (Cabrera, 1936 and Rzasnicki, 1951) have been published and they all advocate a reduction of the number of recognised forms. Ansell (1967) and Sidney (1965) are mainly followed regarding the taxonomy and distribution of Equidae in Africa.

EQUUS ASINUS LINN., 1758 WILD ASS

Only two living subspecies are listed by Ansell (1967), they are *E. asinus africanus* and *E. asinus somalicus*. The former, known as the Nubian wild ass occurs between the Nile and the Red Sea hills between 17° and 21° N (Sidney, 1965). The latter, the Somali wild ass, has become extremely rare and occurs in isolated localities in Abyssinia (Sidney 1965).

EQUUS GREVYI OUSTALET, 1882 GREVY'S ZEBRA

This zebra is characterized by the numerous, narrow black and white stripes covering the body, it is also larger than the other zebras. The Grevy zebra is endemic to the Somali Arid zone. It is confined to parts of Kenya, Ethiopia and Somalia.

EQUUS BURCHELLI GRAY, 1824 BURCHELL ZEBRA

This species is grouped into four sub-species by Ansell (1967) who follows Cabrera (1936). The four sub-species recognized are the following:

E. burchelli burchelli Gray, 1825. Extinct in the Orange Free State but specimens belonging to the nominate form may still occur in Natal.

E. burchelli antiquorum Hamilton Smith, 1884. Distributed from Zululand, Transvaal across Botswana to northern South West Africa and southern Angola. In this sub-species the shadow stripes are normally numerous, the legs are more or less striped below elbow and stifle, but never completely so (Sidney, 1965).

E. burchelli selousi Pocock, 1897. Occurs in central and northern Mozambique; eastern Rhodesia, Malawi and westwards to the Luangwa Valley. Shadow stripes are very few and frequently absent, with the legs striped to the hoofs. Stripes and interspaces on neck and body are narrow and numerous; cervical stripes number 10 to 13, while the vertical stripes number four to eight (Sidney, 1965).

E. burchelli böhmi Matschie, 1892. This sub-species occurs northwards from the middle Zambezi, Luangwa and Rovuma Rivers. In this sub-species the shadow stripes are also few and frequently absent, with the legs striped to the hoofs. Stripes and interspaces on neck and body are wider and less numerous; cervical stripes number seven to ten, while the vertical stripes number from three to four (Sidney, 1965).

EQUUS ZEBRA LINN., 1758 MOUNTAIN ZEBRA

This species, apart from small numbers in southern Angola, is restricted to South West Africa and the Cape Province. Ellerman *et al* (1953), distinguish this species from *Equus burchelli* on the following characteristics.

	Equus zebra	*Equus burchelli*
i.	"Gridiron" pattern on rump.	No "gridiron" pattern.
ii.	Dewlap present.	Dewlap absent.
iii.	Large ears.	Small ears.

Equus zebra has been divided into two subspecies :

Equus zebra zebra Linn., 1758. Cape mountain zebra. This subspecies is confined to the Cradock district and the northern slopes of the Outeniqua Mountains.

Equus zebra hartmannae Matschie, 1898. Hartmann zebra. Its distribution in South West Africa is discussed in great detail in Chapter 1.

The differences between these two subspecies is listed by Sidney (1965) as follows:

> The Hartmann zebra differs from the Cape mountain zebra in being larger in every respect and may be compared with a horse, while the Cape mountain zebra resembles a donkey. The dark and light stripes of the Hartmann zebra are of equal width, with the light ones being slightly wider on occasion.

CHAPTER 1.

HABITAT PREFERENCE, DISTRIBUTION AND STATUS.

1.1 HABITAT PREFERENCE.

1.1.1 Physiography of the distribution area of the Hartmann zebra.

South West Africa may be divided into three major physiographic zones. They are:

(i) the inland plateau to the east, which forms part of the greater sub-continental plateau of southern africa. The plateau region covers approximately 4/5 of the whole of South West Africa. This inland plateau is drained mainly endoreically; in the north and north-west by various drainage lines into the Etosha salina; in the north-east by various omurambas into the Okavango River; and in the central and south-eastern parts by the Nossob and Auob Rivers - which both flow into the Molopo River.

Only two rivers, both seasonal, drain areas of this inland plateau into the sea: in the north the Ugab River and in the south the Fish River. The latter flows into the Orange River which in turn flows into the Atlantic ocean. Perennial waterholes in this region are relatively scarce.

(ii) the escarpment zone to the west of the inland plateau. This zone consists mainly of a mountainous transition area stretching from the inland plateau to the pre-Namib flats. Almost all of the rest of the rivers, all seasonal, in South West Africa originate in this transitional mountain zone. The larger of these rivers, such as the northern Koichab, Hoarusib, Huab, Omaruru, Swakop and Kuiseb Rivers, drain exoreically into the ocean. Most of the smaller ones, such as the Munutum, Sechomib, Tsondab, Tsauchab, Nam and Southern Koichab Rivers, drain endoreically into inland vleis and pans or just disappear in the dunes. This mountainous zone also has relatively many perennial waterholes, situated mostly in the riverbeds.

(iii) the Namib desert, which covers the region between the Atlantic Ocean and the foot of the escarpment zone. In its northern half the desert consists of pediplains, with dunes mainly in the proximity of the coast. South of the Kuiseb River, dunes cover the desert from the coast almost to the foot of the escarpment zone. The inland portion of the Namib desert (sometimes known as the pre-Namib) receives scattered showers during some summers. Perennial waterholes are virtually non-existent in this area.

1.1.2 Habitat preference.

Hartmann zebra occur only in the abovementioned mountainous transition zone. No mention in reports or publications from as early as 1836 onwards could be found of them ever having been observed anywhere else but in this rather restricted area. This clearly illustrates a preference for this broken, mountainous zone. The reasons for this preference are not clear and several factors may contribute in varying degree to this. The more obvious of these are the following:

(i) As has already been mentioned, the mountainous zone is rich in permanent waterholes. It was determined during the study that the Hartmann zebra is confined to water and must drink at least daily during the summer months. It would therefore seem that the availability of surface water is an important limiting factor in their distribution.

(ii) The vegetation of the escarpment zone differs markedly from that of the plateau as well as from that found on the Namib flats. The vegetation types found on the escarpment zone may thus include most of the qualifying aspects regarding availability of preferred foodplants.

(iii) The broken terrain offers protection against weather extremes and man. The Hartmann zebra has so many evolutionary adaptations to a broken habitat that it would appear that they were restricted to this area long before the advent of man. These adaptations include a heart which is on the average ,907 kilogram heavier than the heart of a Burchell zebra. The hoofs of the Hartmann zebra also grow extremely fast and if they are kept in captivity their hoofs must be trimmed regularly. It would therefore seem that the former is more applicable in this case. That they use the mountainous terrain to ameliorate the influence of climate is clearly seen in their behaviour and will be discussed elsewhere.

(iv) No other large grazer reaches the same numbers as the Hartmann zebra in this arid mountainous zone. Other large mammals in this zone are kudu (mainly browsers) and klipspringers (also browsers to a large extent). Their only grazing competitors are the gemsbok and even they, being adapted to the sandy plains on the plateau or Namib flats, never attain large numbers in this region.

Although Hartmann zebra occur from the Orange River in the south to north of the Kunene River in southern Angola, they reach their highest densities in the Khomas Hochland escarpment zone to the west of Windhoek, despite the fact that human interference owing to intensive farming in this region, was and is markedly higher here than anywhere else in the distribution zone. In the Khomas Hochland they have been hunted mercilessly during the last two decades. Despite this, they still are more than twice as numerous in the Khomas Hochland than in the rest of their distribution areas combined.

This fact indicates that they must formerly have been much more numerous in the Khomas Hochland area than anywhere else. It appears that the Khomas Hochland escarpment is the centre of their distribution, with their numbers tapering off to the south and north. This in turn indicates a marked preference for this region. Again we are confronted with the problem as to the reasons for this preference.

Three factors may be important in this context namely topography, climate and vegetation.

(i) Topography. If one looks at a map showing the topography of South West Africa the following is noticeable. Whereas elsewhere, the escarpment zone is either a gradual change from pre-Namib to inland plateau - such as the area to the north of Swakop River, or a quick change from almost true escarpment to inland plateau - such as the area from the Therons and Zaris mountains southwards, in the central region, between the Swakop River and the Naukluft mountains, the mountainous transition zone is backed up by a broken highland - the Khomas Hochland. It is possible that this virtual "hinterland" may have had an influence on the distribution pattern of the Hartmann zebra.

(ii) In consideration of the fact that the distribution of the Hartmann zebra in South West Africa covers approximately a thousand miles from Latitude 17° S to Latitude 28° S, some differences in climate must exist. Marked fluctuations in temperature occur. Summers have very high temperatures in the sun, but strong radiational cooling occurs after sunset. Winter temperatures are fairly low (often near freezing) at dawn but rise rapidly after sunrise. The rainfall isohyets run more or less parallel to the coast. No apparent macro-differences in climate from the Kunene River in the north to the Orange River in the south exist. It would, therefore, seem as though climate in itself is not a serious limiting factor.

(iii) Vegetation is the only other factor that changes appreciably from north to south. To the north of the Ugab River the vegetation in the mountainous transition belt consists chiefly of Colophospermum mopane in various growth forms and in various associations with other plants. In the extreme south where the winter storms of the western Cape sometimes influence the climate drastically, another change in vegetation is apparent. The trees and woody shrubs of the central region give way to succulents and karroid shrubs.

As the vegetation seems to be one of the most important factors in determining the distribution of the Hartmann zebra, also because of the high numbers of these animals on the Khomas Hochland and escarpment, the vegetation of this region is discussed at some length.

1.1.3 Vegetation of the Khomas Hochland.

The Khomas Hochland lies to the west of Windhoek. Although the Naukluft mountains are separate from the highlands they nevertheless form biogeographically an integral part of this region. The vegetation of the Khomas Hochland is classified by Giess (1971) as a highland savanna and in the west the escarpment vegetative zone. The use of the term savanna has been the source of disagreement amongst many botanists. In this study Giess is followed in his classification and use of this term. This is in accordance with Stocker (1964) who suggested that the term savanna should not be limited to a park landscape with single trees, but instead, should be used collectively for forest, parkland and grassland vegetation of tropical climates with pronounced dry periods.

The Khomas Hochland lies between the 100 mm and 350 mm isohyets. The 100 mm isohyet roughly follows the western lower edge of the mountainous escarpment zone whilst the 350 mm isohyet roughly passes through Windhoek. As already mentioned the precipitation occurs mostly in typical thunder showers during a short, sharply defined summer rainy season. This arid climate therefore produces vegetation types adapted to this environment.

During the study it was observed that, although the vegetation of the Khomas Hochland is superficially homogenous, it is actually of a complex and varied nature. The large variety of soils, derived from different parent materials and bedrock, the stratigraphical features of the surfaces, the water-retaining capacities of the various soils, as well as the climatological factors arising from the direction a slope faces and/or height and the angle of slope, all contribute in various degrees to the vegetative characteristics. For the sake of this paper the vegetation is broadly divided into four physiognomic groups and includes the inner edge of the pre-Namib plain because this is also utilized by the Hartmann zebra. The physiognomic groups can be listed as follows:

1.1.3.1 The riparian vegetation.

1.1.3.2 The highland savanna.

1.1.3.3 The escarpment vegetation.

1.1.3.4 The pre-Namib vegetation.

1.1.3.1 The riparian vegetation.

In the area under discussion various types of drainage lines may be discerned. In the east one finds omuramba-like depressions which normally debauch into more sharply defined valleys with steep slopes. To the west, apart from clearly defined rivers such as the Tsauchab, Tsondab, Kuiseb and the Swakop Rivers certain ill-defined drainage lines or washes also form part of the general scene. Despite the physiographic differences the vegetation along these drainage lines shows marked similarities.

The drainage lines are normally marked by the remarkably high and dense tree growth. In the omuramba-like depressions *Acacia karroo*, *A. giraffae* and *Ziziphus mucronata* are the dominant forms. They form a tree storey of anything up to 10 metres high. In the more sharply defined valleys the vegetation is much more varied, especially in areas where perennial water occurs. Apart from the abovementioned trees the following occur as well:

Ficus sycomorus; *Ficus cordata*;
Rhus lancea; *Euclea pseudebenus*; and
Acacia tortilis ssp. *heteracantha*

A second storey along the drainage lines is formed by:

Acacia hebeclada ssp. *hebeclada*;
Phaeoptilon spinosum;
Rhus dinteri; *Tamarix usneoides*; and
Salvadora persica.

No conspicuous ground storey exist but the following plants are the most common,

Ficus guerichiana; *Sansevieria aethiopica*; and
Asparagus nelsii.

Further to the west the abovementioned vegetation grows mostly in the riverbeds instead of lining the banks. One also finds grasses growing in the riverbeds. Along the sandy washes *Acacia tortilis* and *A. giraffae* are the dominant trees, while *Pechuel - Loeschea leubnitziae* also occurs in larger numbers.

As an example of this type of vegetation the vegetation in the Tsondab River bed on the farm Abbabis south of Solitaire is given in Table 1.1. This is where this river opens on to the pre-Namib plain.

TABLE 1.1

THE RIPARIAN VEGETATION OF THE TSONDAB RIVER.

Tall tree strata - approximately 10 metres high.

Species.	height.	diameter of crown.
Acacia tortilis ssp. heteracantha	10 metres	6 metres
Ficus sycomorus	10 metres	12 metres
Ficus cordata	8 metres	5 metres

Lower group of trees and arborescent shrubs:

Ziziphus mucronata	5 metres	10 metres
Adenolobus garipensis	5 metres	3 metres
Euclea pseudebenus	5 metres	10 metres
Boscia albitrunca	4 metres	6 metres
Acacia mellifera ssp. dentinens	4 metres	3 metres
Tamarix usneoides	4 metres	6 metres
Maerua schinzii	3 metres	6 metres

Shrubs:

Boscia foetida	2,5 metres	5 metres
Pechuel-Loeschea leubnitziae	2,5 metres	1 metres
Calicorema capitata	,8 metres	2,5 metres
Rhigozum obovatum	1 metres	1,1 metres
Maytenus heterophylla	2,0 metres	2,8 metres

Grasses:

Stipagrostis obtusa

Stipagrostis namaquensis

Other:

Epiphyte *Plicosephalus curviflorus* on *A*. *tortilis* ssp. *heteracantha* and a green climbing vine-like *Cadaba aphylla* in *Ficus sycomorus*.

1.1.3.2 The highland savanna.

As already stated the taller tree growth normally only occurs along the drainage lines. Away from the drainage lines the vegetation is mostly stunted - with exceptions, and consist mostly of low scattered scrub separated by patches of bare ground and/or patches of grass. Small shrubs occur but are mostly non-succulent and the dominance of the various species varies from community to community. As can be expected, the vegetation, especially the taller trees and shrubs, shows a marked variation from the eastern part of the plateau towards the west. This variation consists mostly of a change in species composition.

The most prominent tree on the sloping hills of the Khomas Hochland is *Acacia hereroensis* . This tree is endemic to the Khomas Hochland and grows on the average about 4 metres high. Although most of the trees are stunted, in sheltered areas they grow higher. Other trees on the ridges towards the eastern side of the highland are:

Ozoroa crassinervia and *Combretum apiculatum*. Both the *Acacias* and *Combretums* show a marked browse line as well as extensive damage caused mainly by kudu (*Tragelaphus strepsiceros*). Farther west *Acacia erubescens* occurs in large numbers. *Maerua schinzii*; *Albizzia anthelmintica* and *Boscia albitrunca* are also present.

The tall shrub layer is formed by:
Acacia mellifera ssp. *detinens*; *A. hebeclada* ssp. *hebeclada*; *A. reficiens*; *Euclea undulata* in coppice-like stands. Other shrubs that occur are:

Acacia senegal var. *rostrata*;
Phaeoptilon spinosum;
Boscia foetida;
Croton subgratissimus;
Elephantorrhiza suffruticosa;
Catophractes alexandri;
Rhigozum trichotomum and several others.

Smaller shrubs also occur, the most common one throughout the Khomas Hochland being *Monechma genistifolium*. Owing to the low humus content and lime richness of the soils in certain areas, the most common here are karroid-like shrubs *Leucosphaera bainesii*; *Leucas pechuelii*; further to the west *Eriocephalus ericoides*; *Walafrida paniculatum*; *Selago albida*; *Antizoma capensis*; *Pteronia mucronata*; and *Thesium lineata*. On certain slopes in the west the resurrection plant *Myrothamnus flabellifolia* is very conspicuous. *Asparagus nelsii* occurs in certain localities.

Some of the more common herbs are:

Sesamum capense;
Felicia muricata;
Pentzia calva;
Blepharis obmitrata;
Dicoma macrocephala
Lantana dinteri;
Euryops subcarnosa;
Hermannia abrotanoides;
Geigeria ornivata;
Amaranthus thunbergii

TABLE 1.2 SPECIES COMPOSITION AND BASAL COVER OF THE GROUND LAYER IN THE DAAN VILJOEN GAME RESERVE.

Grasses	Conventional wheelpoint			Nearest plant	
	Basal strike	% Rel. frequency	% cover	No. times nearest	% Rel. frequency
Enneapogon cenchroides	15	13.8	1.5	134	13.4
Rhynchelytrum sp.	10	9.2	1.0	110	11.0
Anthephora pubescens	7	6.4	.7	98	9.8
Aristida meridionalis	5	4.6	.5	97	9.7
Aristida adscensionis	10	9.2	1.0	87	8.7
Cenchrus ciliaris	20	18.5	2.0	57	5.7
Monelytrum luederitzianum	3	2.7	.3	55	5.7
Stipagrostis uniplumis	3	2.7	.3	57	4.7
Heteropogon contortus	2	1.8	.2	38	3.8
Eragrostis echinochloidea	5	4.6	.5	28	2.8
Pogonarthria fleckii	0			25	2.5
Fingerhuthia africana	0			20	2.0
Eragrostis rotifer	2	1.8	.2	18	1.8
Microchloa caffra	2	1.8	.2	15	1.5
Eragrostis trichophora	0			13	1.3
Schmidtia bulbosa	2	1.8	.2	12	1.2
Cynodon dactylon	1	.9	.1	10	1.0
Eragrostis porosa	0			9	.9
Eragrostis nindensis	1	.9	.1	8	.8
Hyparrhenia hirta	0			7	.7
Eragrostis machrochlamys	0			7	.7
Triraphis sp.	0			6	.6
Eragrostis superba	0			5	.5
Digitaria eriantha	1	.9	.1	5	.5
Eragrostis lehmanniana	0			4	.4
Chloris virgata	0			3	.3
Eragrostis scopelophyla	0			2	.2

TABLE 1.2 Continued

Herbs.

Monechma genistifolium	6
Fimbristylis sp.	3
Gnidia polycephala	2
Oxalis sp.	0
Tribulus terrestris	2
Geigeria ornativa	1
Dicoma macrocephala	1
Amaranthus thunbergii	1
Trichoneura grandiglumis	1
Gomphocarpus tomentosus	1
Blepharis obmitratra	1
Junchus sp.	0

Basal strikes recorded : 108

% basal cover : 10.8 per cent.

5.5	.6	25	2.5
2.7	.3	18	1.8
1.8	.2	9	.9
		7	.7
1.8	.2	5	.5
.9	.1	5	.5
.9	.1	4	.4
.9	.1	3	.3
.9	.1	2	.2
.9	.1	1	.1
.9	.1	1	.1
		1	.1

TABLE: 1.3 SPECIES COMPOSITION AND DIFFE
MOUNTAIN PLATEAU.

Species
Eriocephalus dinteri
Wellstedia dinteri
Barleria kaloxytona
Leucosphaera bainesii
Monechma genestifolium
Calicorema capitata
Maytenus heterophylla
Thesium lacinulatum
Rhus volkii
Aptosimum lineare
Blepharis spinifex
Boscia foetida
Euclea asperrima
Asparagus nelsii
Kleinia longiflorus
Rhigozum obovatum
Indigofera candidissima
Cyphostemma sp.
Blepharis obmitrata sp.
Antizoma capensis
Solanum sp.
Phaeoptilon spinosum
TOTAL

RENTIATION OF THE SHRUB LAYER ON THE NAUKLUFT

No. quadrats of occurance	No of plants	Relative frequancy (F) %	Relative dominance (D) %	Importance value (F+D)
16	129	16.1	19.0	35.1
12	285	12.1	41.9	54.0
12	42	12.1	6.2	18.3
8	47	8.1	6.9	15.0
8	41	8.1	6.1	14.2
6	42	6.1	6.3	12.3
6	34	6.1	5.0	11.1
6	4	6.1	0.6	6.7
5	12	5.1	1.7	6.8
3	23	3.0	3.4	6.4
3	5	3.0	0.7	3.7
2	2	2.0	0.2	2.2
1	3	1.0	0.4	1.4
1	2	1.0	0.2	1.2
1	1	1.0	0.1	1.1
1	1	1.0	0.1	1.1
1	1	1.0	0.1	1.1
1	1	1.0	0.1	1.1
1	1	1.0	0.1	1.1
1	1	1.0	0.1	1.1
1	1	1.0	0.1	1.1
1	1	1.0	0.1	1.1
99	681	99.9	99.6	199.5

Three aloes, *Aloe littoralis*; *A. viridiflora* and *A. hereroensis* also occur on the Khomas Hochland.

The variety of grasses one encounters in this area is remarkable More than 30 different species were found during the study. Wheelpoint surveys of 1,000 points each were carried out at both the Daan Viljoen Game Reserve and the Naukluft Mountain Zebra Park. Owing to the low basal density the nearest plant to the point was also noted. A further advantage of this method is that more of the grasses in the area are recorded than would have been the case if only strikes were recorded. This data were used to get an idea of the species composition. It was found that the most dominant perennials were *Rhynchelytrum repens* and *Anthephora pubescens*. The abnormally large size of the *Cenchrus ciliaris* tufts are the reason for the relatively high number of strikes on this species.

1.1.3.3 The escarpment vegetation.

The broken, mountainous transition belt of the escarpment is appreciably drier than the two vegetation zones already discussed. The change in vegetation is therefore not unexpected. Although most of the components already mentioned in the two previous vegetative zones still occur, several others also make their appearance now. The more important is the larger variety of Commiphora species present whereas in the Highland savanna only *C. pyracanthoides* occur. The various slopes in the escarpment area present an even more diverse number of plant communities.

The most conspicuous plant species present here are *Moringa ovalifolia*; *Aloe dichotoma*; several *Commiphora* species viz. *Commiphora saxicola*; *C. angolensis* ; *C. glaucescens*; *C. virgata*; *Euphorbia virosa* which forms almost pure stands on certain slopes, *Adenolobus garipensis* and *Sterculia africana*.

Botanical surveys were carried out on various slopes in the Naukluft Mountain zebra Park. The following tables give an idea of the trees and shrubs present as well as their growth form.

TABLE 1.4

VEGETATION ON A SIXTY DEGREE NORTH-FACING SLOPE OF BLACK DOLOMITE IN THE NAUKLUFT MOUNTAIN.

Open woodland of small trees and scattering of brush.

Plant species.	height	diameter of crown	% foliage density.
Commiphora species	6 metres	5 metres	30
Moringa ovalifolia	7 metres	7 metres	10
Boscia albitrunca	3 metres	2 metres	40
Monechma genistifolium	0,3 metres	0,5 metres	60
Montinia caryophyllacea	1 metres	1 metres	20
Adenolobus garipensis	5 metres	5 metres	20
Rhus marlothii	2 metres	3 metres	30
Thesium cf. lineatum	1 metres	0,3 metres	30

TABLE 1.5

VEGETATION ON A FORTY TO SEVENTY DEGREE SOUTH-FACING SLOPE, PARTLY BEDROCK, PARTLY THIN SOIL LIGHTLY VENEERING THE BEDROCK IN THE NAUKLUFT MOUNTAIN.

Open cover of low shrubs, with scattered taller, almost arborescent shrubs.

Plant species.	height	diameter of crown.	% foliage density.
Rhigozum trichotomum	1 metres	1 metres	50
R. obovatum	3 metres	3 metres	60
Phaeoptilon spinosum	2 metres	2 metres	70
Boscia albitrunca	4 metres	3 metres	70
Sansevieria aethiopica	0.3 metres	0.3 metres	70
Acacia hereroensis	3 metres	2 metres	30
Myrothamnus flabellifolia	.80 metres	.10 metres	90
Adenolobus garipensis	.2 metres	2 metres	30
Euphorbia virosa	2 metres	2 metres	60
Boscia foetida	3 metres	2 metres	50
Ficus cordata	3 metres	2 metres	50
Catophractes alexandri	2 metres	2 metres	30
Monechma genistifolium	5 metres	8 metres	70
Acacia mellifera ssp. detinens	2 metres	2 metres	40
Montinia caryophylacea	1 metres	1 metres	20
Kleinia longiflorus	1 metres	1 metres	50
Grewia bicolor	1 metres	1 metres	40

A wheelpoint survey was also carried out on the lower slopes of the escarpment region in the Naukluft Mountain Zebra Park. This gives one a good indication of the basal cover and species composition of the grass layer. The higher percentage basal cover recorded as opposed to that recorded at the Daan Viljoen Game Reserve can be ascribed to the very low biomass in this game reserve. This is further augmented by the fact that the Hartmann zebra have not yet utilized the lower slopes.

Other features are that several grass species occur here but not at the Daan Viljoen Game Reserve. Also that although the percentage relative frequency of the plants present in both areas differ considerable two species viz. , *Enneapogon cenchroides* and *Eragrostis nindensis* are still quite prominent in the Naukluft Mountain Zebra Park. The grasses present in the latter Park are normally lower down on the succession phase and with the perennials, the tufts are smaller.

1.1.3.4 The pre-Namib vegetation.

The pre-Namib stretches from the foot of the rocky slopes of the escarpment region westward for approximately 20 to 30 km. The western border of the pre-Namib zone is difficult to define, but it is approximately where the perennial vegetation *between* the sandy washes terminates.

Along the eastern sides of the pre-Namib plains one finds alluvial fans built up of coarse material washed down from the escarpment regions. In other areas large plains are formed with sheet calcrete just below the surface or broken up into calcrete rubble. The vegetation here consists mainly of shrubs and scattered trees. The dominant trees are *Maerua schinzii* ; *Parkinsonia africana* and *Boscia albitrunca*. The shrub are mainly *Catophractes alexandri*; *Commiphora virgata*; *Calicorema capitata*; *Boscia foetida*; *Rhigozum trichotomum*; *Kleinia longiflorus*; *Leucosphaera bainesii*; *Leuchas pechuelli*; *Cadaba aphylla* and *Euphorbia lignosa*.

TABLE: 1.6 SPECIES COMPOSITION AND BASAL COVER OF THE GROUND LAYER IN THE LOWER SLOPES OF THE NAUKLUFT MOUNTAIN ZEBRA PARK.

Grasses	Conventional wheelpoint			Nearest plant	
	Basal strike	% Rel. frequency	% cover	No. times nearest	% Rel. frequency
Eragrostis ninensis	27	19.3	2.7	215	21.5
Enneapogon cenchroides	38	27.1	3.8	164	16.4
Aristida adscensionis	32	22.8	3.2	152	15.2
Aristida effusa	8	5.7	0.8	78	7.8
Enneapogon brachystachyus	13	9.2	1.3	75	7.5
Eragrostis porosa	3	2.1	0.3	69	6.9
Eragrostis annulata	5	3.5	0.5	63	6.3
Rhynchelytrum sp.	2	1.4	0.2	43	4.3
Stipagrostis uniplumis				42	4.2
Anthephora pubescens				26	2.6
Stipagrostis ciliata				13	1.3
Tragus beteronianus	3	2.1	0.3	8	0.8
Stipagrostis obtusa				8	0.8
Fingerhuthia africana				7	0.7
Cenchrus ciliaris				6	0.6
Eragrostis echinochloidea				3	0.3
Aristida curvata				2	0.2
Pongonarthria fleckii				2	0.2
Digitaria eriantha	1	0.7	0.1	2	0.2
Heteropogon contortus				1	0.1
Hyparrhenia hirta				1	0.1
Herbs					
Monechma genistofolium	3	2.1	0.3	8	0.8
Blepharis obmitrata	3	2.1	0.3	3	0.3
Geigeria ornativa	1	0.7	0.1	2	0.2
Oxalis sp.	1	0.7	0.1	2	0.2

Basal strikes recorded : 140
% basal cover : 14.0 per cent.

In good rainfall years the grasses are much the same as in table 1.6. On the sandy flats, however, one finds almost pure stands of Stipagrostis ciliata and S. obtusa.

1.2 DISTRIBUTION.

The main distribution of the Hartmann zebra lies within the borders of South West Africa. No Hartmann zebra occur to the south of the Orange River in the Richtersveld apart from small parties that may infrequently cross the river. Sidney (1965) quoting Lang mentions that a small number of Hartmann zebra occurred at Kamieskroon, at approximate Latitude 31° S in 1912. This is approximately 260 km. south of the Orange River. No other records of the existence of this zebra further south could be found. Sidney (1965) also considers the Kamiesberg as their most southern distribution limit. Considering their clearly preferred habitat in the Khomas Hochland, as well as the sharp decline in number from here towards the south (and north) its seems highly unlikely that they ever reached high numbers to the south of the Orange River.

The furthest north-west that the other subspecies, Equus zebra zebra, ever occurred according to available records (Sclater, 1900) was on the Cedarberg in Piquetberg. From this it would seem as though the tw subspecies have been isolated for at least a century, probably much more.

Hartmann zebra have been reported as far north as Mossamede in Angola (Bocage, 1890). Today their distribution in Angola is limited to the Iona Game Reserve immediately to the north of the Kunene River.

In South West Africa they are distributed today in four more or less isolated localities. These localities will be discussed separately. (also see map).

1.2.1. The northern concentration.

Although politically the Kaokoveld only lies to the north of the Hoanib River and to the west of Ovamboland, the area to the north of the Ugab River can zoogeographically be considered the same entity. The Ugab River forms a migration route to the east, for Hartmann zebra occur all along it as far as the farm Ozema, 138, close to Outjo, Longitude 16° E. Nowhere else do they occur so far inland as along the Ugab River. From the Ugab River they occur northwards along the escarpment zone to the Kunene River. South of the Hoanib River they are mostly restricted to the west of the farming areas.

1.2.2 Erongo mountains.

The population of Hartmann zebra in the Erongo mountains is rather restricted. They occur all over the mountains but especially on the eastern and south-eastern slopes.

1.2.3 The central concentration.

The bulk of the Hartmann zebra population in South West Africa occurs within the region from the Swakop River southwards along the escarpment as far south as Theronsberg in the Zaris mountain range. They only occur eastward onto the Khomas Hochland along the Kuiseb and Gaub drainage systems as far as the farms Jonkersgrab and Tara. A large concentration remains on the Naukluft mountain range.

1.2.4 The southern concentration.

In the south the Hartmann zebra are almost exclusively limited to the Fish River Canyon and the Huns mountains immediately to the west.

1.3 STATUS.

No other large mammal in Southern Africa has been so ruthlessly persecuted during the last two decades in South West Africa as the Hartmann zebra. At one stage only 20 years ago it must have been one of the most numerous of the larger wild mammals still left in Southern Africa. According to 15 independent reliable sources, mostly farmers and Government officials, between 50 000 to 75 000 of these animals still occurred on the central concentration area during the early 1950's. They were systematically hunted and various stories of how one hundred or more were killed during hunts in this area are common.

During 1960 the Nature Conservation and Tourism Division, with the help of the South African Police, made a survey of the status of game in South West Africa. This survey took the form of a questionnaire which was distributed and collected by the police on farms in their districts. Information gathered from this questionnaire showed that 10 700 Hartmann zebra were left on farming areas in South West Africa. In 1968 an aerial survey was carried out by the Nature Conservation and Tourism Division, from the Kunene River in the North to the Orange River in the South. During this survey only 5 500 Hartmann zebra were counted on farming areas. These figures include a 27 per cent correction factor which was determined by flying over the Daan Viljoen Game Reserve with its known number of Hartmann zebra.

With the abovementioned figures in hand one may follow the tren shown by the Hartmann zebra population in South West Africa. The figure of 50 000 that was estimated in 1950 for the central concentration area (Khomas Hochland), can be taken for argument's sake as the total Hartmann zebra population for the whole of their distribution area on farms. In 1960, only ten years later, the figure of 50 000 had already dropped to 10 700 and by 1968, to only 5 500 in the farming area. This decline in Hartmann zebra numbers is especially disturbing if viewed against the fact that it was declared specially protected in 1933.

The total number of Hartmann zebra in South West Africa according to the 1968 survey was approximately 7 000. A breakdown of this figure shows the following distribution:

1.3.1 The northern concentration.

In this region there were still approximately 1500 left, the largest concentration of Hartmann zebra being south of the Hoanib River and west and south of Otjovasandu. In this region there were still about 1 100 of these animals left, with another 360 north of the Hoanib River, mostly north of Hoarusib River. Farther south about 100 animals still occurred along the Ugab River on farming land.

1.3.2 The Erongo mountain.

Here the animals are very much restricted by the isolated mountain and fences. No more than approximately 100 animals occur in this region.

1.3.3 The central concentration.

As mentioned previously the bulk of the Hartmann zebra population in South West Africa occurs in this region. The 1968 survey showed approximately 5 300 of these animals in this area, distributed in the Khomas Hochland escarpment and a number in the Namib Desert Park. This figure includes the Naukluft mountains where 800 animals were counted with a further 300 in the Theronsberg area of the Zaris mountains.

1.3.4 The southern concentration.

In this area only 200 Hartmann zebra, probably fewer, remain.

As can be seen from the distribution analysis of Hartmann zebra in South West Africa approximately 80 per cent of the total population, occur on farming land. Here they compete with livestock for living requirements and the serious problems they create during drought years, will increase in future. Measures to safeguard their survival are therefore urgently needed.

CHAPTER 2.

ECOLOGY.

2.1 METHODS.

2.1.1 Influence of climate.

The Daan Viljoen Game Reserve is situated, as the crow flies, 14 kilometres from Windhoek. There is no appreciable difference in altitude. Windhoek possesses a large meteorological station where various measurements viz. relative humidity, strength and direction of wind and temperature are taken on an hourly basis. It was therefore decided to use this information in conjunction with the behavioural work being done at the Daan Viljoen Game Reserve to determine the influence of climatic factors on the Hartmann zebra. For the figures delineating grazing, only observations made during 1970 are used. Each figure is based on one day each month so that the specific activity, temperature and relative humidity for that particular day could be correlated.

2.1.2 Influence of insects.

At half-hour intervals the irritation caused by insects was measured by counting the number of times an animal twitched its tail in one minute. For accuracy a stopwatch and tally counter were used. This was done with three animals, selected at random, in a group.

2.1.3 Determination of digestibility.

This experiment was carried out on three Hartmann zebra stallions kept solitary in quarantine pens at the Daan Viljoen Game Reserve These pens all had concrete floors which were washed every morning. Each holding pen had a small enclosure with a connecting door. During th pre-experimental period the animals were trained to leave the holding pen when the connecting door was opened every time after they defaecated.

Basically this digestion experiment involved a record of the lucern hay consumed and the amount voided in the faeces. The faeces collected represented quantitatively the undigested residue of the measured amount of lucern hay consumed. The digestibility experiment lasted 26 days, which may be devided in a pre-experimental period of 15 days and an experimental period of 11 days. During the first 15 days the animals were fed on lucern hay. The quantity for each animal was determined by the animal's weight and the assumption that the lucern hay contained 56 per cent totally digestible nutrients - as described by Morrison (1961) for horses. This period served to condition the animals to this ration and also to clean the digestive tract of other material.

During the experimental period the animals were fed the allotted ration every morning at 8 a.m. for 10 days. A sample was collected every morning from the lucern hay before it was weighed into the three rations. These samples were kept in plastic bags to prevent further moisture loss. The moisture present in each sample was later determined in Windhoek.

The dung was collected manually every time an animal defaecated over 24 hours a day. This was then put in a plastic bag and numbered. After 24 hours - normally just after the Hartmann zebra was fed in the morning the bags were weighed to determine the amount of wet dung voided by each animal during the previous 24 hours. The last bags were weighed on the morning of the 11th day. Every animal's dung for a specific 24 hour period was then sun dried and weighed again. A sample of this dung was then taken and oven dried at 80^{o} C for 24 hours to determine the moisture content of the dung. The oven-dried dung, together with the dried lucern hay samples, was then sent to Stellenbosch where it was analysed.

2.1.4 Blood and urine samples.

During the study period prof. G. Louw accompanied the author on a hunting trip on which eight animals were shot. A blood sample was taken from a large vein in the body as soon as possible after the animal had been shot. Before collecting the sample the interior of the syringe was rinsed in heparine. The heparinized blood sample was centrifuged immediately for two minutes at 5000 r.p.m. The supernated serum was drawn off with automatic push button pipet~~s~~te, transferred to vials and stored at -10° C. Urine samples were taken aseptically with a sterile disposable syringe, transferred to vials and stored in a similar manner until analysed.

2.2 THE INFLUENCE OF CLIMATE.

Owing to the lack of instruments and facilities to measure microclimate it is difficult to assess the influence of climatic factors on the behaviour of the Hartmann zebra in a more than general way. This study will therefore deal only briefly with the innumerable possible combinations of those physical factors which may have an effect on the behaviour pattern. The Hartmann zebra is so well-adapted to changes in its habitat brought about by changing physical factors that only very subtle changes in its activity pattern were observed. Furthermore it is only because of the repetitive nature of some of these 'subtle changes' in its behaviour that one can, albeit with a certain amount of hesitance, try to link them to the annual changes in climate. In this regard, the physical factors that cause the most marked change in its activities are temperature and rainfall.

2.2.1 Temperature.

2.2.1.1 The influence of temperature on nutritional activities.

From the 12 figures (figures 2.1 to 2.12) depicting the grazing patterns and daily temperatures for the various months no dramatic change is immediately visible. On studying the figures more closely however, three factors that maybe due to an influence by the temperature come to one's notice:

(i) The grazing patterns for the colder months (June, July and August) are not as irregular as during the warmer months (October, November, December and January). During these latter months the grazing intensity is initially very high, being higher than 70 per cent at first light. It is followed by a number of high peaks during the day, with periods in between of very low grazing intensity. Bligh and Harthoorn (1965) in East Africa have shown with the aid of radio telemetry that animals lose much body heat while standing inactively in the shade. This irregular grazing pattern shown by Hartmann zebra during the hot months could be an adaptation. The animals graze in the sun until their body temperatures reach a peak after which they retir into the shade to lower their body temperature.

(ii) The daily temperature at first light has an apparent effect on the intensity of grazing at this time of the day. During June, July and August the temperatures fall to below 20° C at daybreak. In each case only about 40 per cent of the animals under observation grazed at first light. During the rest of the year the percentage of animals actively grazing at first light is well over 50 per cent.

(iii) Another interesting aspect is the change in the time of highest grazing intensity during the various months of the

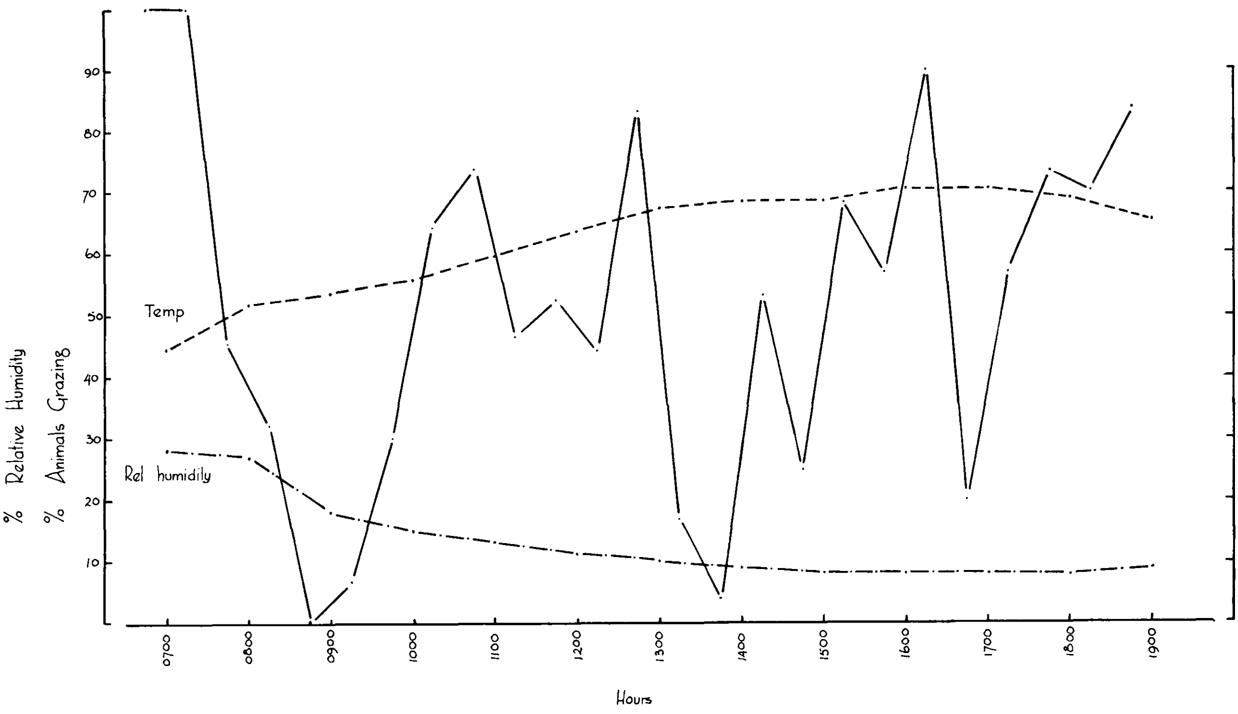


Figure 2.1: Grazing Pattern for January

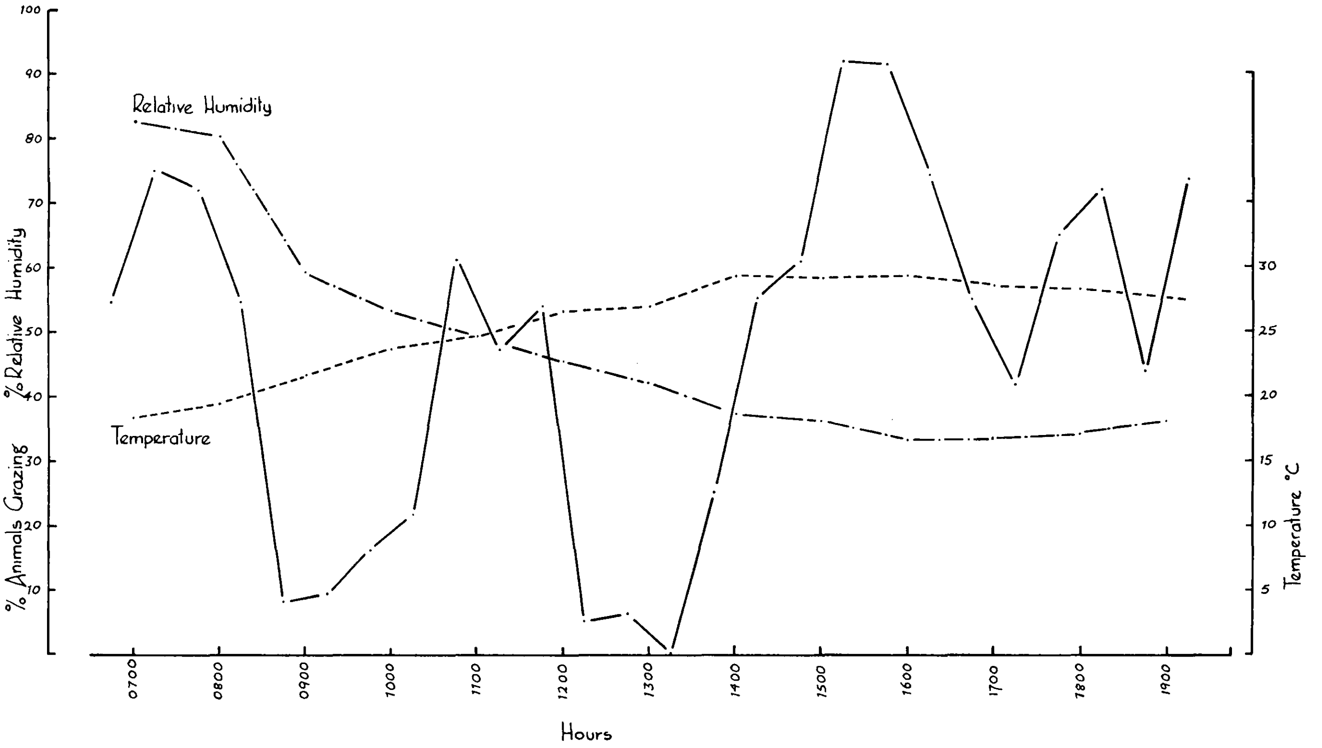


Figure 2.2: Grazing Pattern for February

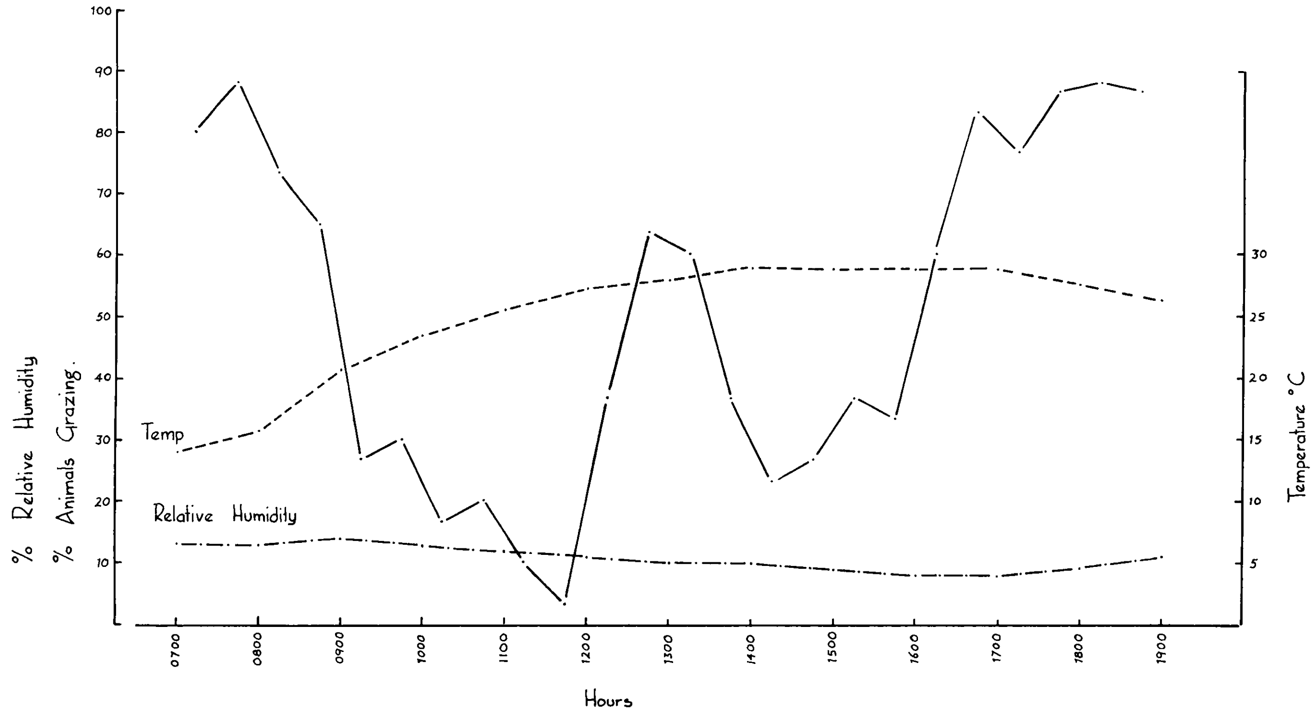


Figure 2.3: Grazing Pattern for March

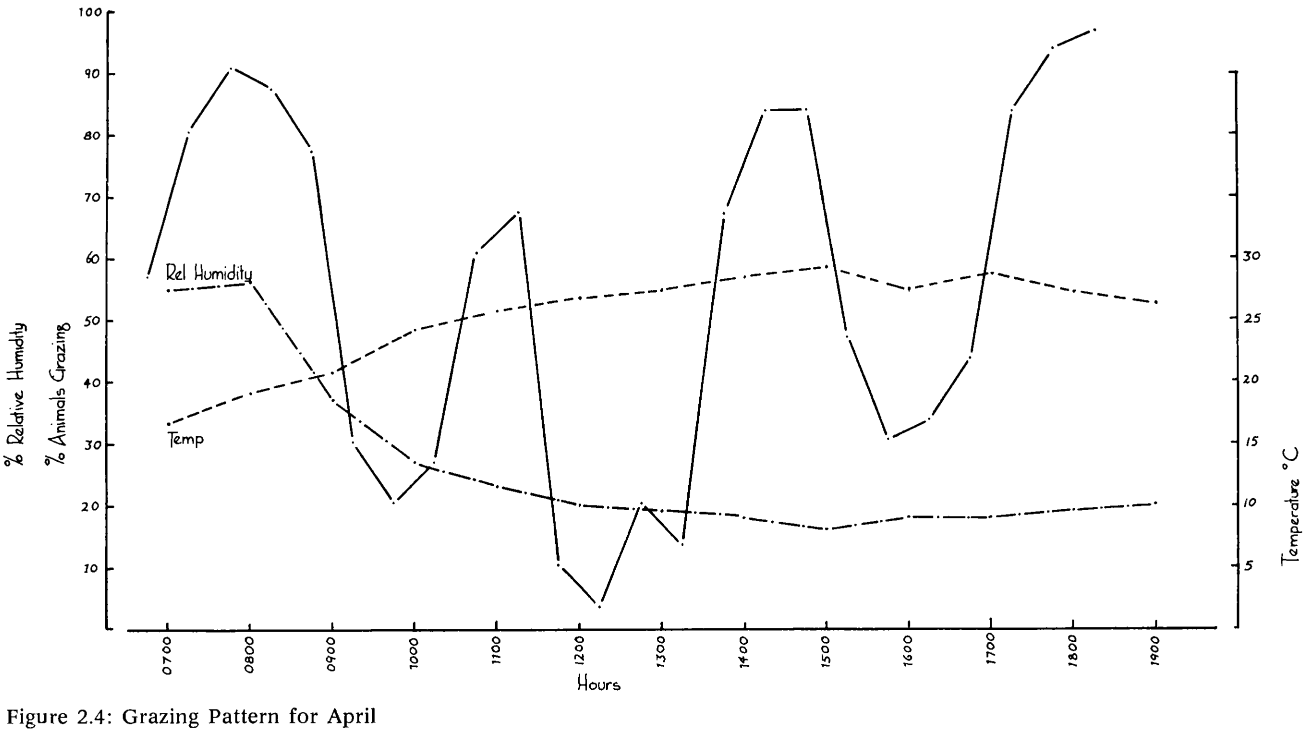


Figure 2.4: Grazing Pattern for April

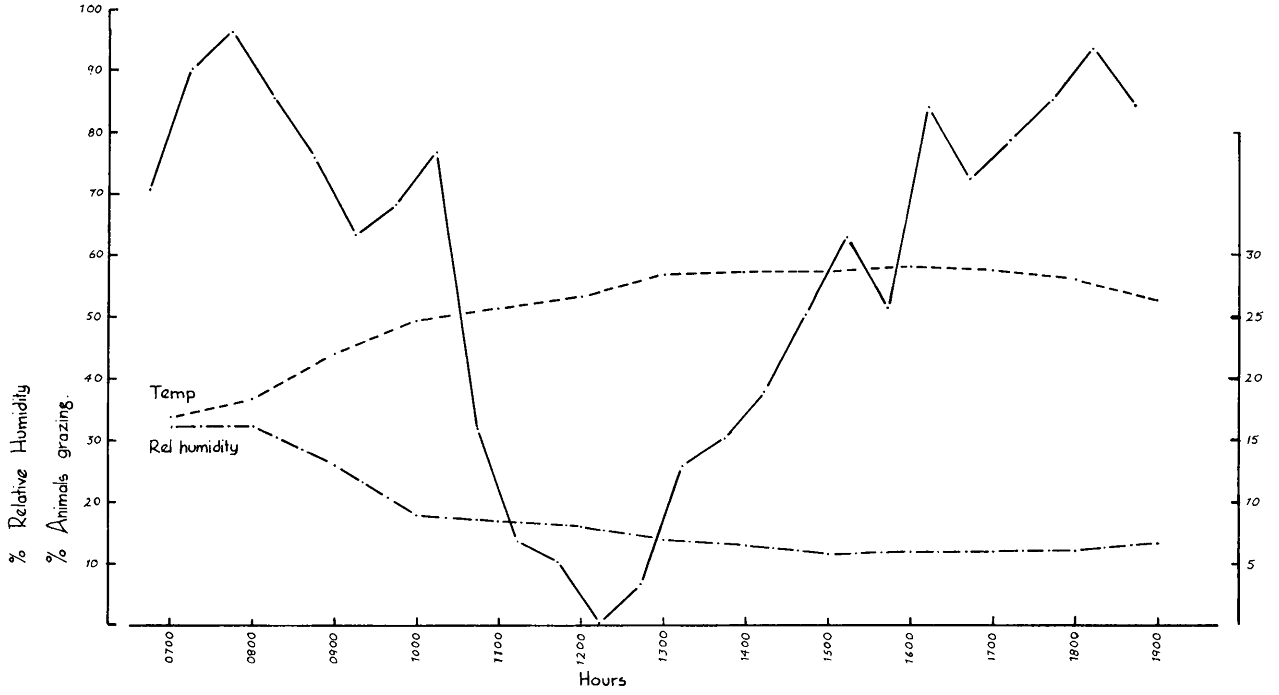


Figure 2.5: Grazing Pattern for May

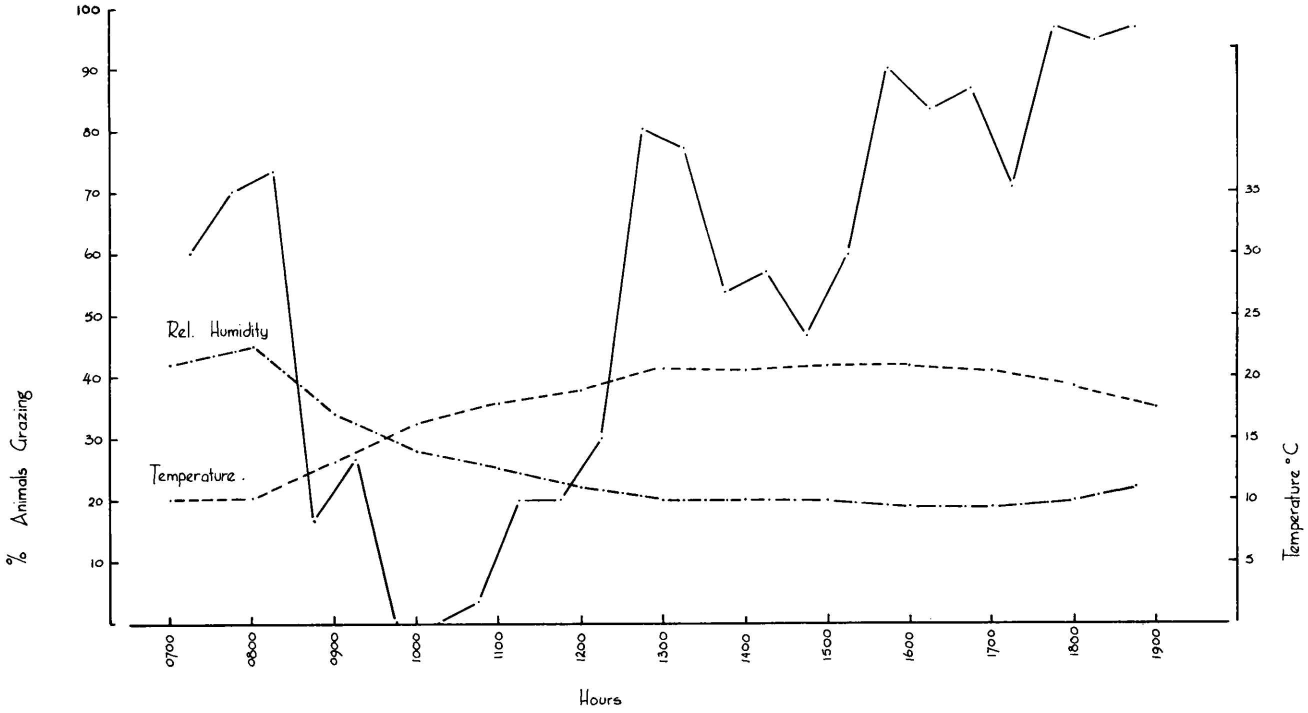


Figure 2.6: Grazing Pattern for June

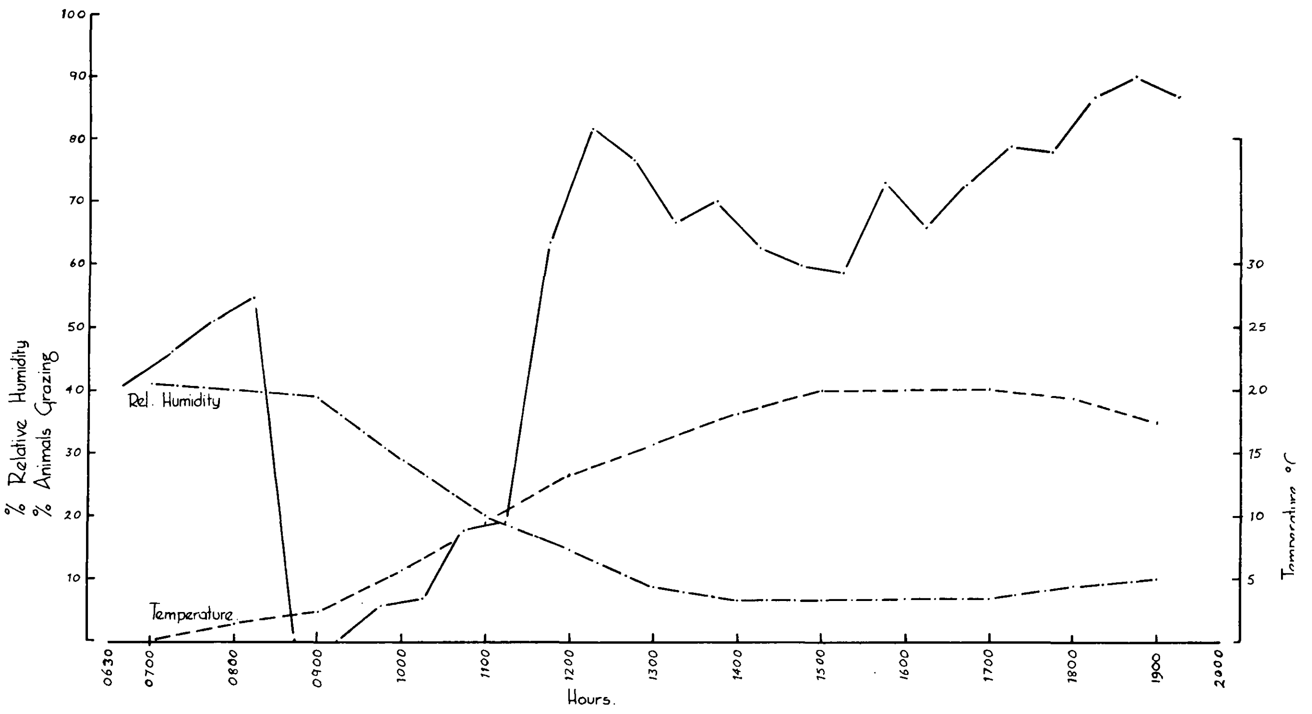


Figure 2.7: Grazing Pattern for July

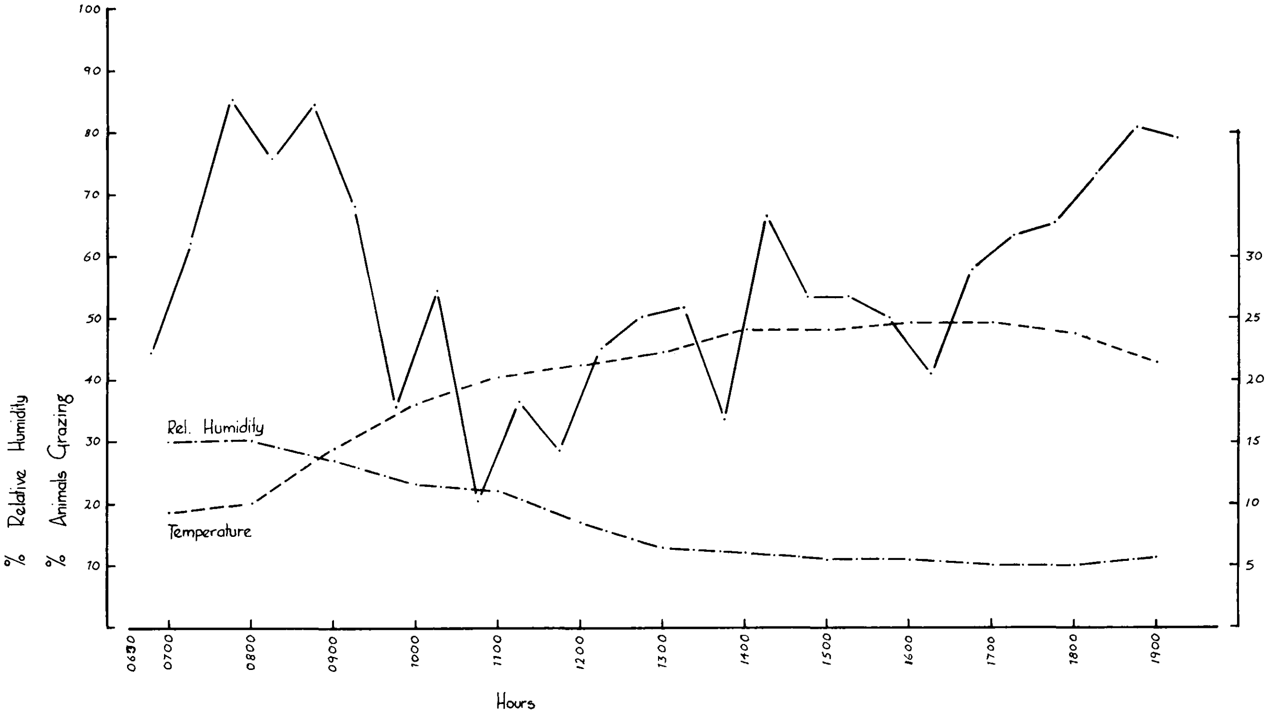


Figure 2.8: Grazing Pattern for August

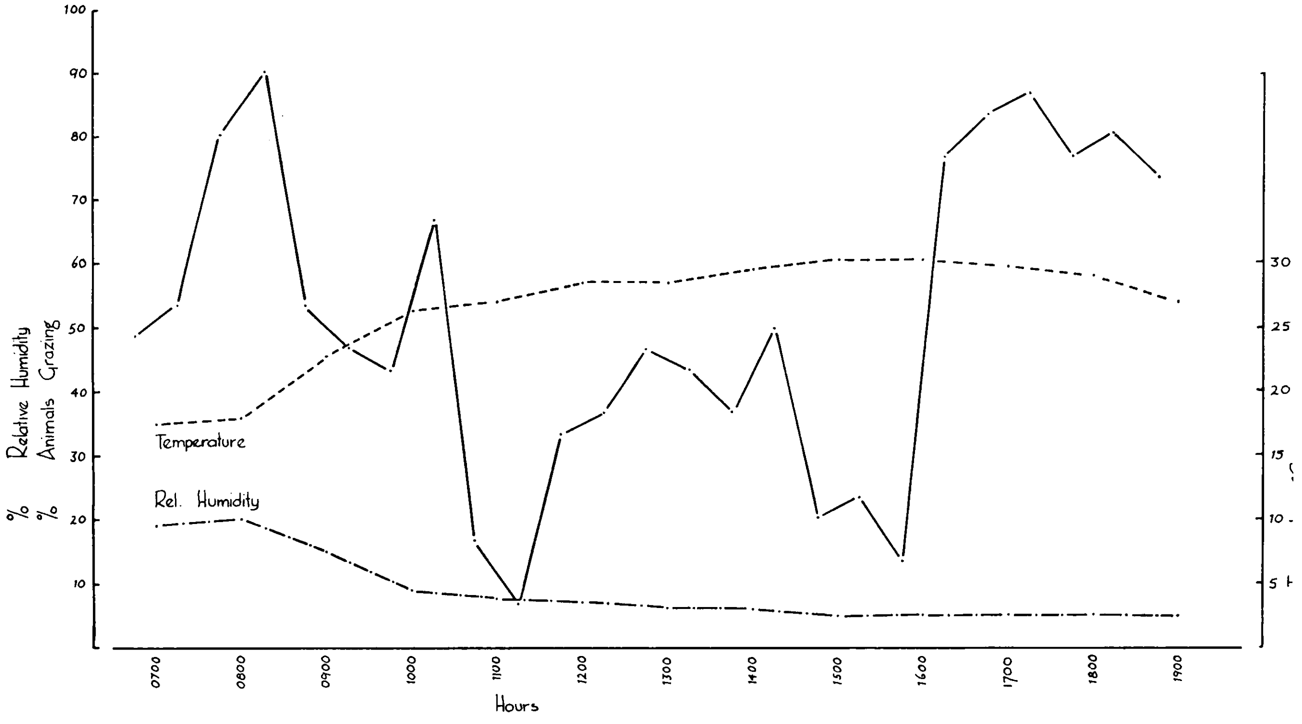


Figure 2.9: Grazing Pattern for September

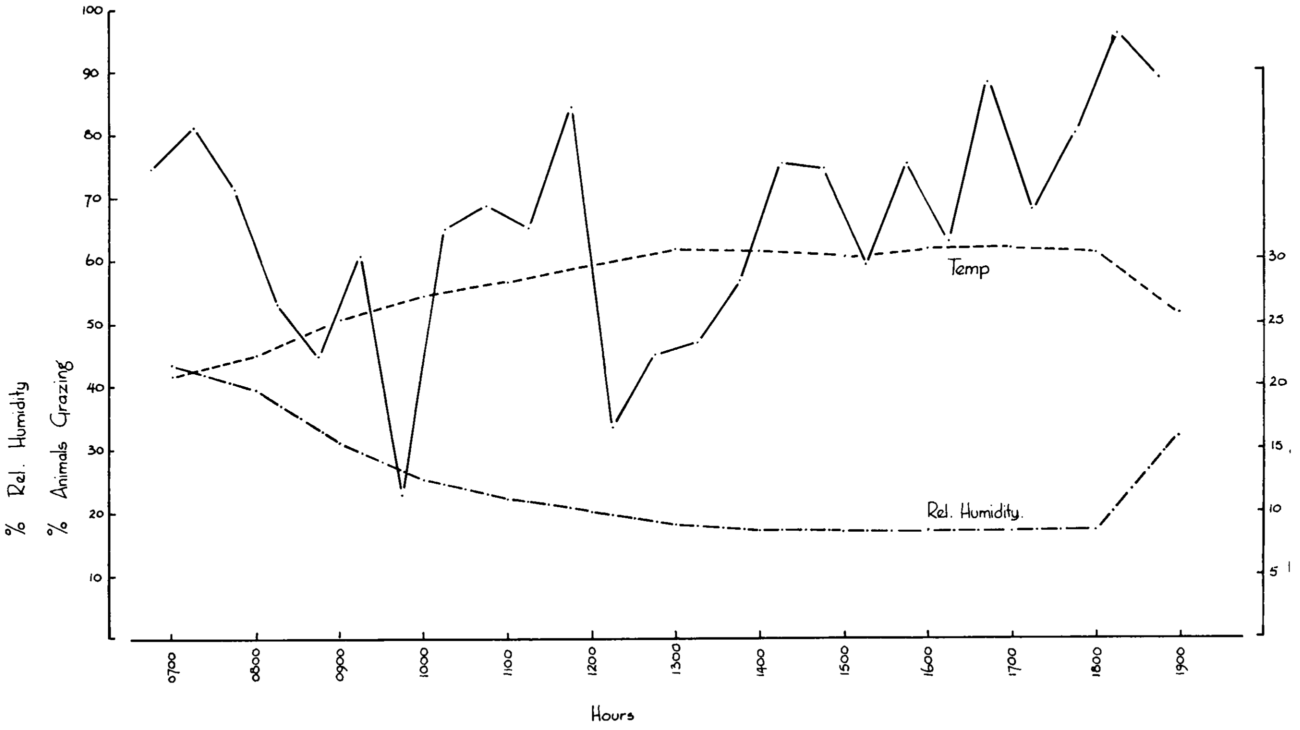


Figure 2.10: Grazing Pattern for October (Rain — Green flush)

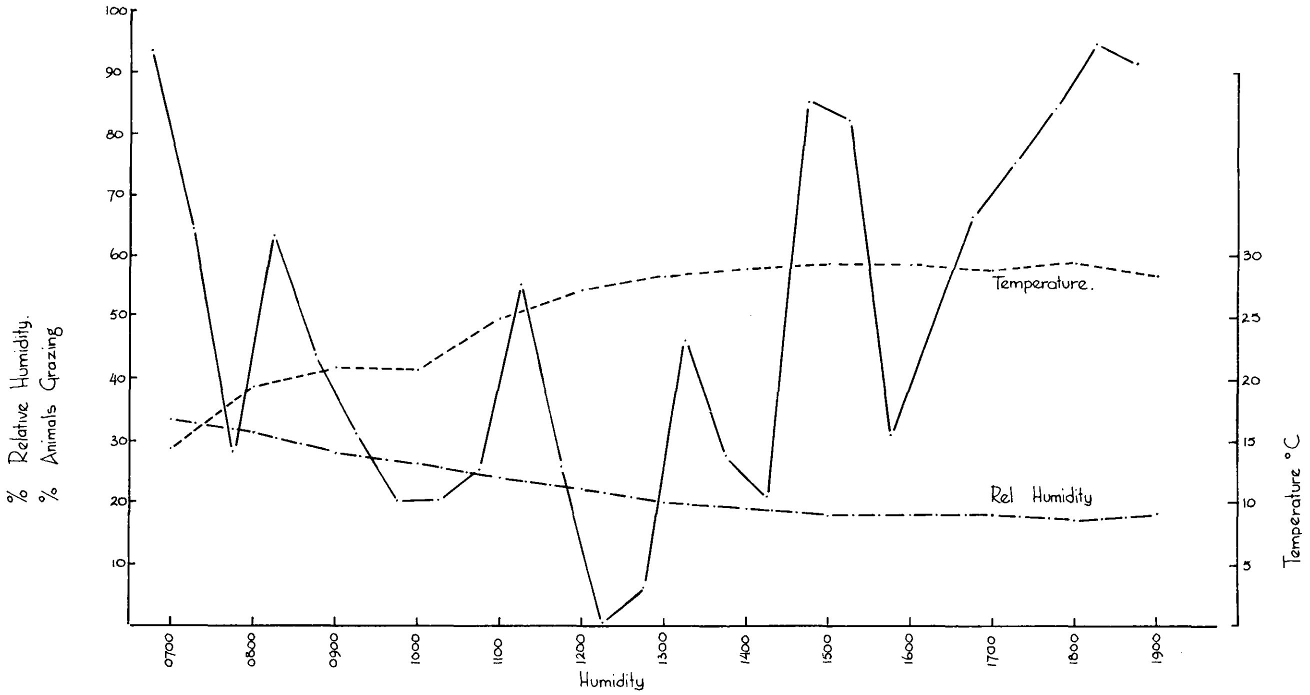


Figure 2.11: Grazing Pattern for November

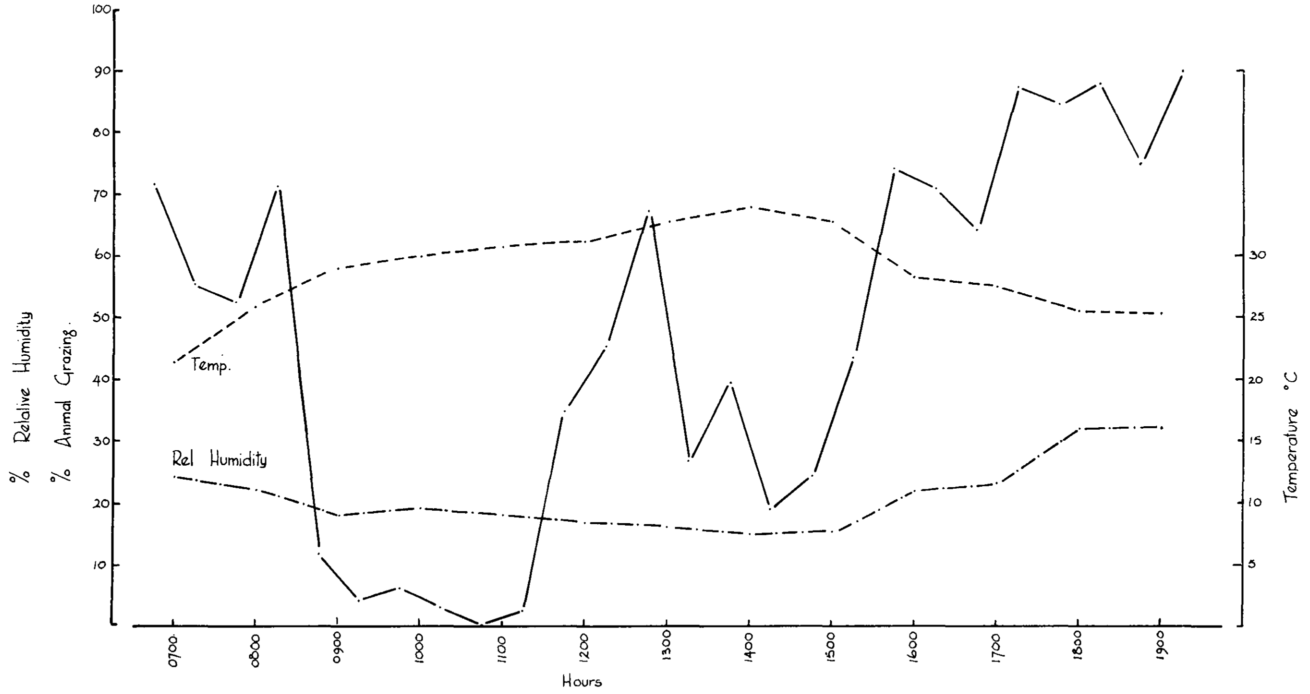


Figure 2.12: Grazing Pattern for December

year. During the more temperate months of April, May and September about an equal amount of very high intensity grazing takes place during the morning and afternoon. During the cold months of June, July and August after an initial burst, apparently just to satisfy their immediate needs, the animals stand around sunning themselves. As the temperature rises so does the grazing intensity increase. The bulk of the most concentrated grazing takes place during the afternoon.

Despite the fact that the grazing pattern for October is erratic it still has a very high intensity. This is most prol bly due to the flush of green grass on the veld after some showers of rain fourteen days earlier.

During the hot, dry months of October, November and sometime December, the Hartmann zebra visit the waterholes at least once a day.

2.2.1.2 The influence of temperature on comfort activities.

There is no significant difference in the total amount of time spe resting during the various season of the year. The percentage of animals seeking shelter in the shade of trees during the different months of the year , on the other hand, shows a very marked difference. As may be seen in figure 2.13 the number of animals seeking shade varies from remarkably high during the warmer months of the year to absolutely none during July.

It is interesting to note that animals resting in the shade also show a definite behavioural pattern. Each individual selects a tree for itself while females are accompanied by their foals. They always distrib themselves one, or in the case of a female with a foal, two to a tree. In order to make full use of the shade of the tree they almost invariably stand in the shade cast by the bole of the tree, facing away from the direction of the sun.

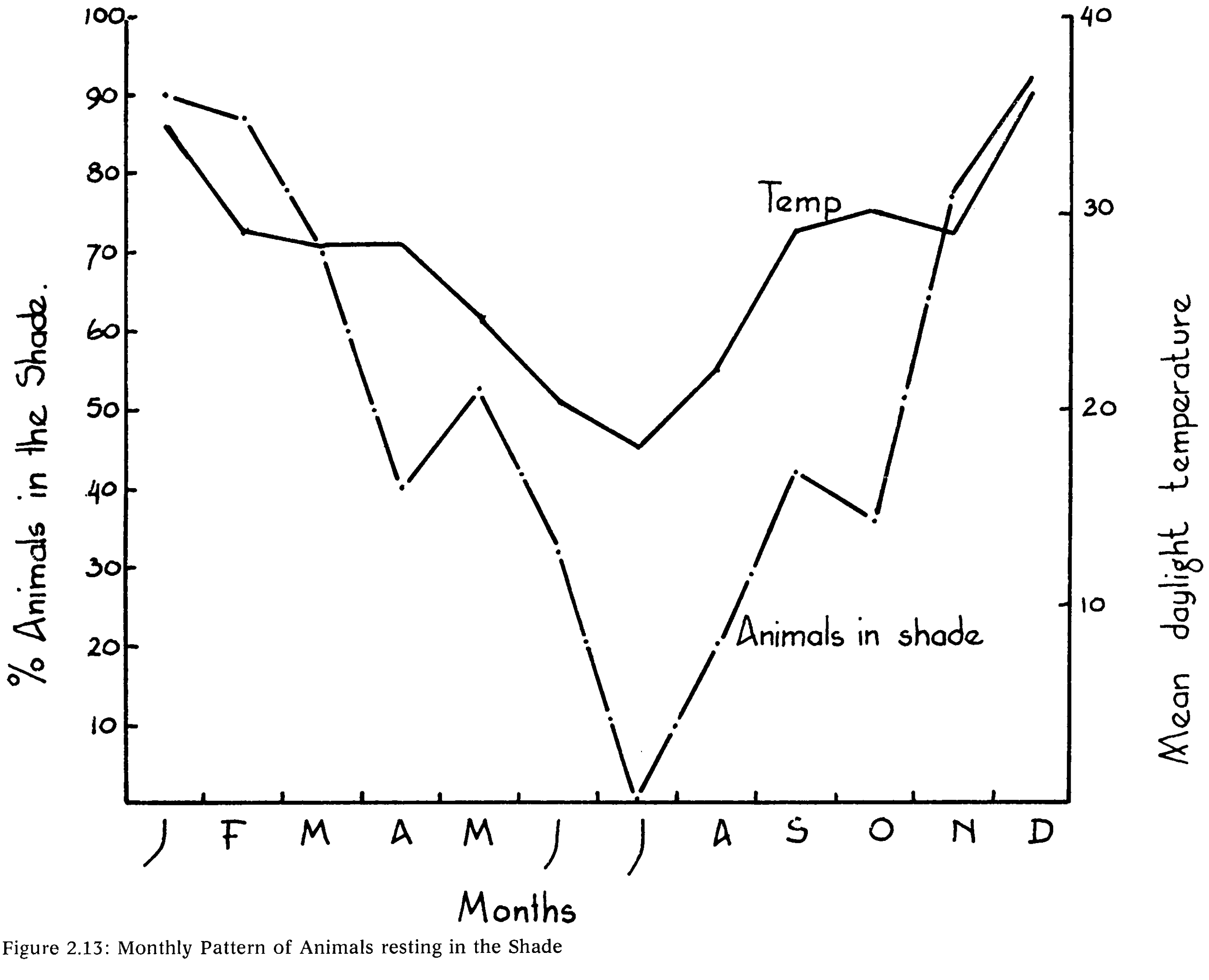


Figure 2.13: Monthly Pattern of Animals resting in the Shade

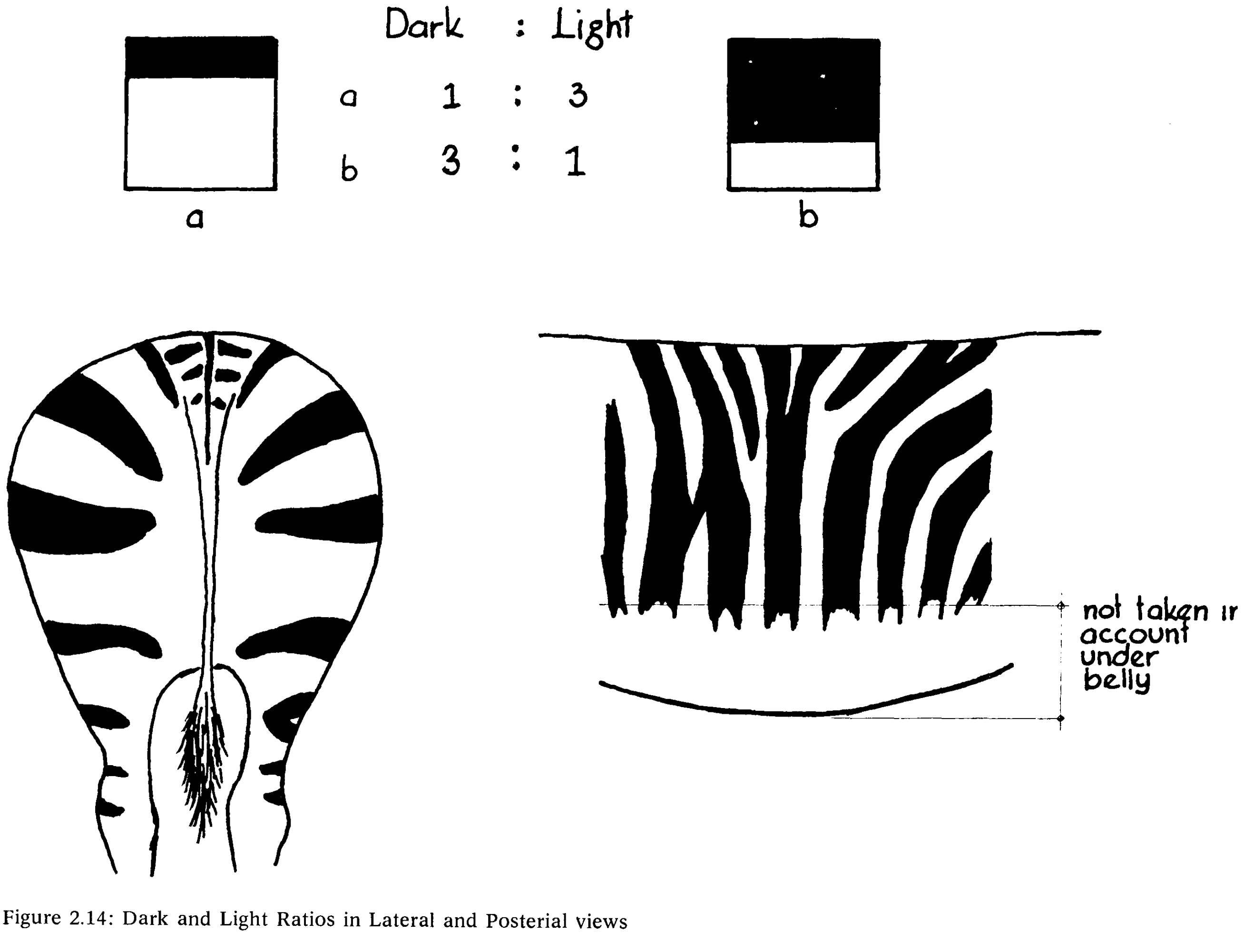


Figure 2.14: Dark and Light Ratios in Lateral and Posterial views

2.2.1.3 Orientation of the body surfaces towards the sun.

It is a well-known fact that black surfaces absorb more heat than lighter coloured or white surfaces. Although no proof exists, it appears from the behaviour shown by Hartmann zebra that this may influence their behaviour. As can be seen from figure 2.14 a Hartmann zebra standing broadside on displays a body surface with a light : dark ratio of 1 : 3. When facing away however, this ratio changes to 3 : 1. This fact, combined with the difference in total body surface when viewed laterally and posteriorly, makes the orientation of body surfaces to physical stimuli an important factor in the adaptation of the Hartmann zebra to their environment.

This behaviour was especially marked during the early mornings of the colder months of the year. During these months they would frequently sun themselves throughout the day at regular intervals especially if the environmental temperature was below approximately 20° C. This orientation of the body to gain maximum absorption of heat, however, was not limited to the winter months. Even during the early mornings of summer months they would sometimes orientate themselves laterally to the rising sun - apparently to raise their body temperature. However, when the environmental temperature rose above approximately 25° C the zebras would normally orientate their bodies with the posterior end towards the sun while grazing. This of course means that more of the lighter shaded body surface for less absorption of heat, is presented towards the su

2.2.2 Relative humidity.

Figures 2.1 to 2.12 also show the relative humidity. Relative humidity has no conspicuous macroclimatic influence on the grazing pattern of the Hartmann zebra.

2.2.3 Rainfall.

The influence of rainfall on the Hartmann zebra is much more obvious than the influence of any of the other climatic factors. The more important of these influences is the way the foaling season of the Hartmann zebra is correlated with the rainy season. (See figure 4.9). Although newly-born foals were observed throughout the year only 14 per cent were not born during the rainy season.

The other influences are more indirect. The rainfall also influences the grazing pattern to some extent. Figure 2.10 shows how the grazing pattern for October, 1970 is influenced by a green flush after rain showers 14 days earlier.

During the rainy season the disturbance factor caused by insects is also very much higher.

2.2.4 Wind.

Wind also has some influence on certain behaviour patterns of the Hartmann zebra. They tend to used the upper third of hill slopes more frequently than the lower two-thirds during the heat of day in warm weather. This is possibly a means of making full use of the cooling effect of breezes. The unpleasantly cold westerly wind in the study area was avoided by grazing on the lee sides of hills.

2.3 THE INFLUENCE OF INSECTS.

During the study it was determined that when Hartmann zebra are disturbed by insects, they (the Hartmann zebra) vigorously switch and twitch their tails. The intensity of this tail twitching may be regarded as an indication of the amount of irritation caused.

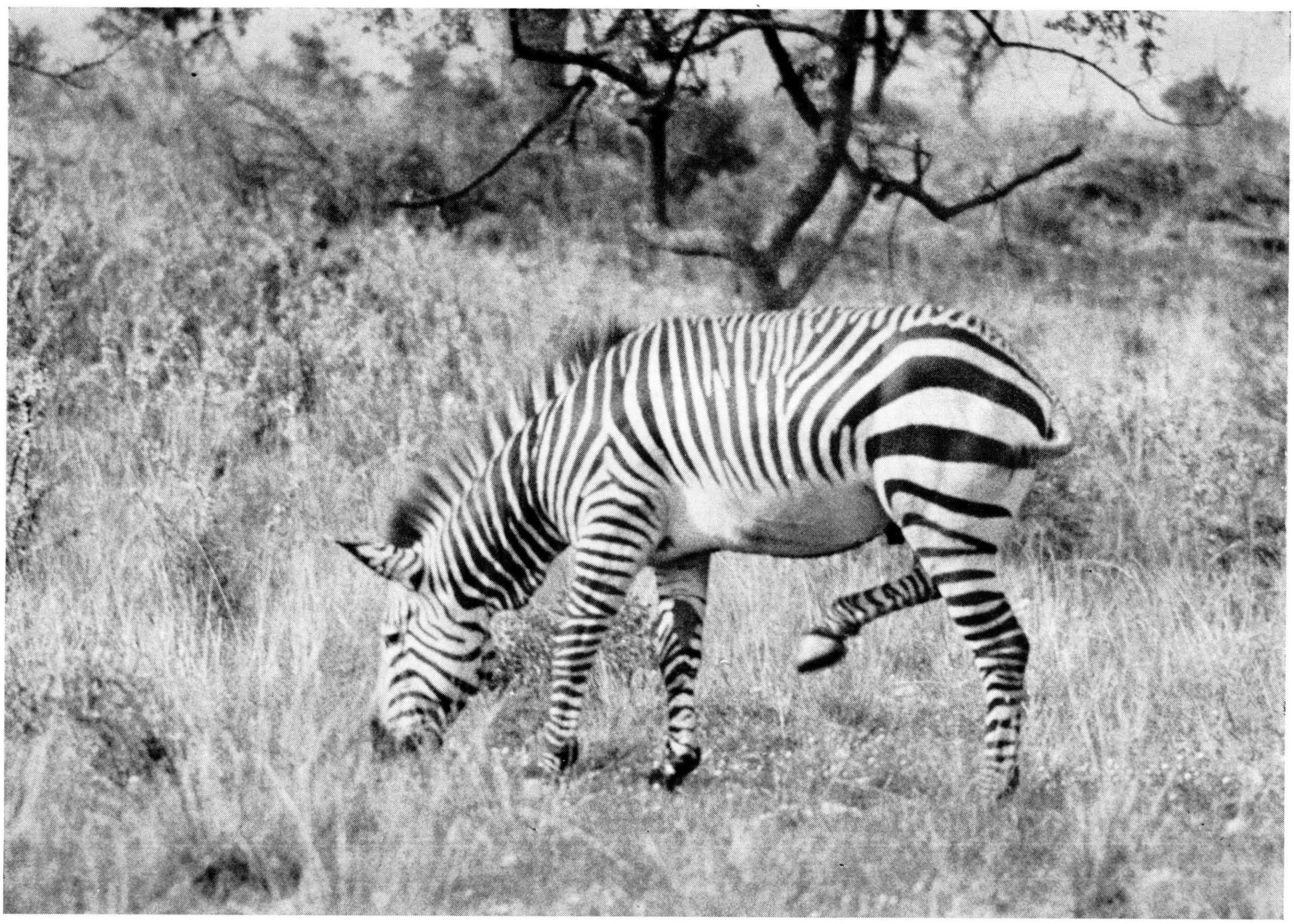


Plate 2: A Hartmann zebra male showing signs of irritation cauzed by insects — switching of the tail and stamping of the feet.

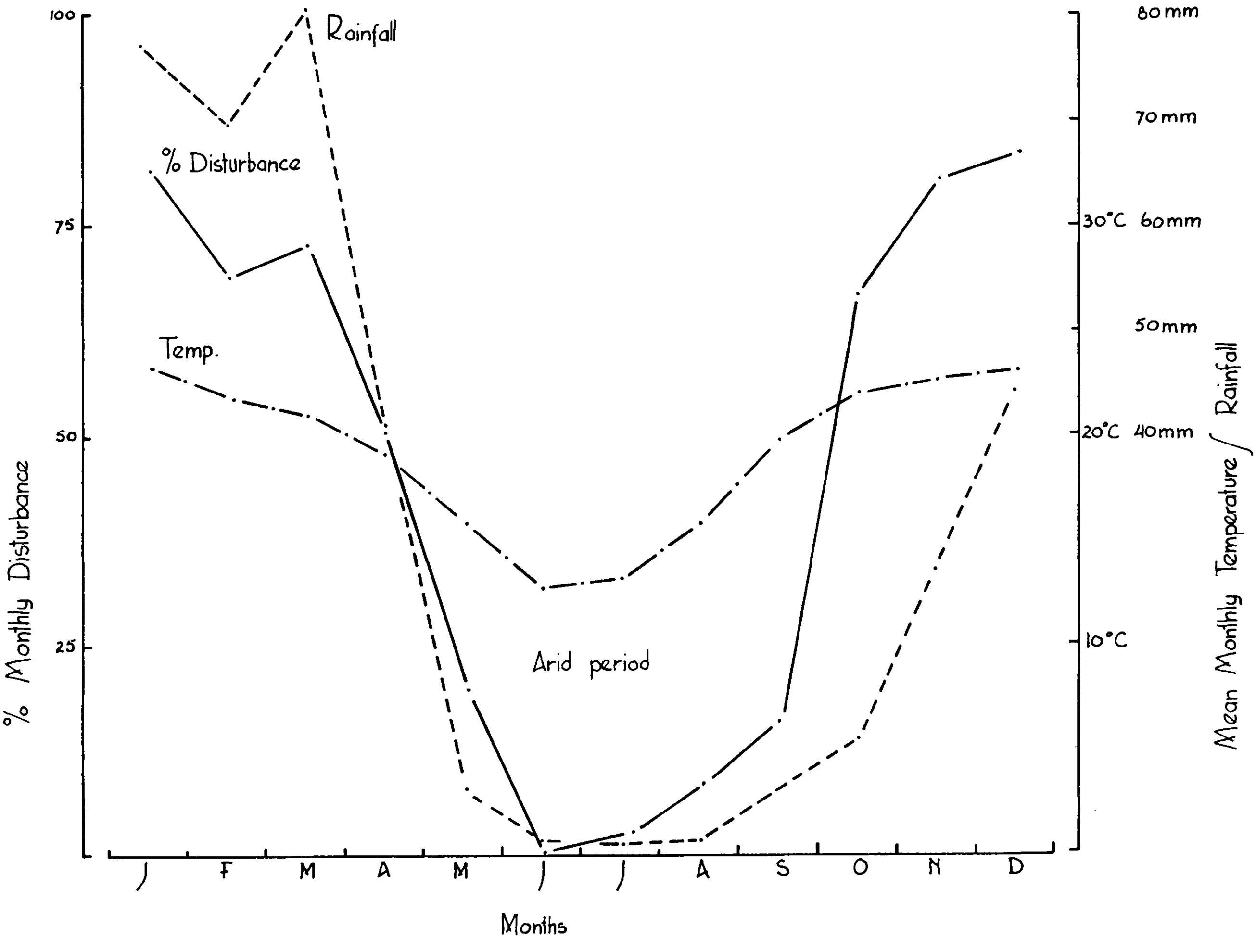


Figure 2.15: Relationship between % Disturbance by Insects and 'arid' period

2.4 DIGESTIVE ABILITIES OF THE HARTMANN ZEBRA.

The Hartmann zebra compete with livestock for grazing and according to popular belief one never sees a zebra in poor condition in a free-living state. Although the author did see Hartmann zebra in poor condition during the drought periods it was decided to determine whether these animals possess better abilities than the horse to digest hay. The experiment was carried out at the Daan Viljoen Game Reserve and the lucern hay and faeces samples were analysed by van der Merwe and Klein, Stellenbosch. The results may be seen below.

TABLE 2.1

DRY MATERIAL (DM) OFFERED, TAKEN AND VOIDED BY *EQUUS ZEBRA HARTMANNAE*.

Animal.	Offered. g	Orts. g	Taken. g	Voided. g
1	53138	3318	49820	24644
2	53138	5550	47588	25902
3	44282	2274	42008	20117

Animals 1 and 2 were both fully grown adults and were offered the same amounts of lucern hay. Animal 3 was a sub-adult and therefore received a smaller ration of lucern hay. The orts (amount not eaten) left by each animal as a percentage of the total amount offered to each individual varied from 6,2 per cent for animal 1 ; 10,4 per cent for animal 2 ; to 5,1 per cent for animal 3. The dry material voided is almost half the weight of the dry material offered to each individual.

The composition of the lucern hay and faeces is given in table 2.

TABLE 2.2

COMPOSITION OF THE LUCERN HAY AND FAECES VOIDED
(ON A MOISTURE FREE BASIS).

		Faeces voided by animal			
	Lucern hay offered.	1	2	3	Average.
Dry material %	88,7				
Organic material %	89,7	82,5	79,8	82,8	
Ash %	10,3	17,5	20,2	17,8	18,5
Crude protein %	16,2	9,4	9,2	10,3	9,6
Crude fibre %	29,5	42,0	40,9	42,2	41,7
Ether extract %	2,1	3,2	3,7	2,7	3,3
*NFE %	41,8	27,9	26,9	27,1	27,3
	99,9	100,0	100,9	100,1	100,4

* Nitrogen free extract.

As may be seen the two important nutrients, indicated by crude protein and NFE, are both absorbed by the experimental animals. NFE shows a difference of 14,5 per cent in the percentage present in the lucern hay and faeces. In the crude protein the difference is not quite as high, being only 6,6 per cent between the percentage present in lucern hay and faeces. As one would have expected the percentage of crude fibre in the faeces is almost 12,2 per cent more that the percentage of crude fibre present in the lucern hay.

For a comparison between the abilities of Hartmann zebra and horses to digest lucern hay see table 2.3 .

TABLE 2.3

A COMPARISON OF THE APPARENT DIGESTIBILITY OF VARIOUS NUTRIENTS BETWEEN HORSES AND *EQUUS ZEBRA HARTMANNAE*.

	Equus zebra hartmannae				Horses		
	Animal. 1	2	3	Average.	*(1967)	*(1970)	Average
Dry material %	50,5	45,6	52,1	49,4	52,1	60,8	56,4
Organic material %	54,4	51,5	56,1	54,3	-	56,4	56,4
Crude protein %	71,6	69,1	69,1	70,1	65,2	75,4	70,3
Crude fibre %	28,8	24,5	31,6	28,3	39,5	39,1	39,3
Ether extract %	26,0	31,0	40,0	32,3	5,0	31,2	18,1
NFE %	67,0	64,8	69,0	66,9	72,2	72,3	72,2

*Fonnesbeck *et al* (1967)

*Van der Noot & Gilbreath (1970)

The three experimental Hartmann zebra showed the ability to digest 49,4 per cent of the dry material (lucern hay). This is lower than the 52,1 per cent found by Fonnesbeck *et al* (1967) or the 60,8 per cent found by Van der Noot & Gilbreath (1970), with an average of 56,4 per cent for the horse. Although only a small number of Hartmann zebra were used in this experiment one may form the conclusion that there are no marked differences in the ability to utilize hay between the Hartmann zebra and the domestic horse (G.N. Louw, pers. com. 1971). It would appear that it does not posses any outstanding qualities in the utilization of natural fodder. From an ecological viewpoint this is important as it show that the Hartmann zebra do need grazing of a relatively high quality with low crude fibre and high crude protein contents. This factor must be taken into consideration when game reserves are established to ensure the survival of the Hartmann zebra.

2.5 DEPENDENCE ON A CONSTANT WATER SUPPLY.

As discussed under daily activity, Hartmann zebra drink daily and sometimes twice daily during the warm arid months. During the rainy season they sometimes drink only every second day but the overall impression is that they are quite dependent on water.

Blood and urine samples taken during the present study were analysed and the results may be seen in table 2.4 . The figures in the first five colums show clearly that the Hartmann zebra does not possess an outstanding kidney function, but if compared with the horse can be considered average (G.N. Louw, pers. com. 1971). This then, bears out observation in the field that they are dependent on a constant water supply.

TABLE 2.4

ANALYSES OF BLOOD AND URINE OF EQUUS ZEBRA HARTMANNAE.

	Osmolality		Haematocrit	Glucose
	(mOsm)		%	mg/100 ml
	Plasma	Urine	Blood	Plasma
Mare 1	292	1287	39	71,27
Mare 2	312	1055	-	77,02
Mare 3	287	1097	34	188,40
Mare 4 (no urine)	311	-	38,5	87,36
MEAN	300	1146	37,2	88,51
Stallion 1	296	1465	30	93,33
Stallion 2	311	1230	38	73,33
Stallion 4	324	1257	-	91,11
MEAN	310	1317	34	85,92

	Inorganic Phosphate		Urea		Lactate
	mg P/100 ml		mg UREA/100 ml		mg/100 ml
	Plasma	Urine	Plasma	Urine	Plasma
Mare 1	4,99	0,34	39,76	3005	31,33
Mare 2	4,17	0,00	38,01	2243	61,92
Mare 3	4,72	2,04	47,13	3050	72,46
Mare 4 (no urine)	5,71		35,20		106,71
MEAN	4,90	0,79	40,02	2766	68,10
Stallion 1	5,51	0,68	63,34	4044	31,24
Stallion 2	4,44	0,34	63,23	2663	72,17
Stallion 3	4,60	0,00	49,20	3867	54,95
MEAN	4,85	0,34	58,59	3525	52,79

CHAPTER 3.

BEHAVIOUR.

3.1 METHODS.

3.1.1 Study areas.

During the research work on the Hartmann zebra in South West Africa four study areas were used. These were:

(i) the Etosha National Park

(ii) the Daan Viljoen Game Reserve

(iii) the Namib Desert Park

(iv) the Naukluft Mountain Zebra Park.

3.1.1.1 The Etosha National Park.

The only region in the Etosha National Park where Hartmann zebr occur is at Otjovasandu, in the extreme western part of the game reserve. Otjovasandu lies on the 1,400 metre contour at the edge of the escarpment, and is only on the fringe of the Hartmann zebra's distribution at this latitude. From here they are spread westwards through the mountainous transition belt to the edge of the Namib desert. It was the only place left in South West Africa where they could migrate unhindered from the mountainous escarpment zone onto the Namib plains after the first summer rains each year. With the implementation of the Odendaal Commission's proposals, the new western boundary runs three miles to the west of Otjovasandu, completely cutting off this Hartmann zebra habitat from the Etosha National Park.

In this study area the following aspects received special attentio

(a) The migratory habits of the Hartmann zebra, where unhindered by obstacles created by man, viz. fences and roads.

(b) The influence of the two zebra species, namely *Equus zebra hartmannae* and *Equus burchelli antiquorum* on each other as their distribution overlaps in this area.

3.1.1.2 The Daan Viljoen Game Reserve.

This game reserve is situated in the eastern region of the Khomas Hochland~~s~~ at an approximate altitude of 1500 metres. By road it is about 28 kilometres from Windhoek, although as the crow flies only about half that distance. The total area of the game reserve is slightly more than 4,000 hectares, but the zebra are confined to just over 1,100 hectares.

This study area was exclusively used for the study of behaviour.

The population of Hartmann zebra in this game reserve is 48. This study area was visited frequently and an average of one week per month were spent here, sometimes considerably more. Each of the zebra became intimately known over three years. Their relationships and the progeny of the various females were also known. This proved to be a great advantage.

The 48 individuals were divided into six breeding units and one bachelor unit which were in existence when the study began. During the study period two new breeding units were established.

3.1.1.3 The Namib Desert Park.

This park is situated inland from Walvis Bay. It covers an area of approximately 12,800 square kilometres. It is bounded in the north by the Swakop River and in the south by the Kuiseb River. Both these rivers are seasonal, but especially the Kuiseb has pools of water that last throughout the dry season. The eastern boundary of the game reserve is fenced off on the pre-Namib flats. The movements of the Hartmann zebra are therefore restricted to the pre-Namib plains in this

This area is populated by approximately 1000 Hartmann zebra but was visited less frequently than the other areas for behavioural studies.

3.1.1.4 The Naukluft Mountain Zebra Park.

This game reserve lies in the mountainous transition belt of the escarpment. It is situated in the Naukluft mountains which form a separate entity, completely separated from the rest of the escarpment by the deeply dissected Koichab and Tsauchab Rivers. Approximately 800 Hartmann zebra inhabit the mountain and move freely all over the area, which is approximately 120 kilometres by 60 kilometres. This game reserve was also visited frequently in order to compare the behaviour of these animals with those in the Daan Viljoen Game Reserve.

3.1.2 Identification.

Owing to a number of reasons it was regarded as impracticable to mark Hartmann zebra with neckbands in the conventional way. Apart from everything else the area west of Otjovasandu is so vast and the terrain so broken that if the animals moved, say only 10 kilometres, it would have been practically impossible to follow them. The same problem occurs in the Naukluft Mountains and to a lesser extent in the Namib Desert Park where they concentrate in the Kuiseb Canyon areas and the extremely broken Swakop River valley - although they sometimes do occur on the gravel plains.

It was therefore decided to apply the method used with great success by Klingel (1967) in East Africa in his studies on Burchell zebra. In the Daan Viljoen Game Reserve with its small number of animals in a relatively small enclosed area a reference collection of photographs was built up. Photographs were taken from both sides of each of the animals in the Game Reserve. The animal on the negative was magnified to fill a postcard which was then stapled onto a 12,6 cm x 20 card. A separate card was kept for each side of each zebra. This left enough space for other data to be written in, for example:

(i) date of photograph - this was especially important in newly born foals as from subsequent photographs the growth rate could be estimated;

(ii) index number of the animal;

(iii) sex of the animal;

(iv) relationship of the animal to other animals;

(v) oestrus dates for female animals;

(vi) date of parturition with female animals;

(vii) weaning dates;

(viii) date on which an animal joined the bachelor group;

(ix) date on which an animal established its own breeding group.

These cards and photographs were carried in a 'Tickler' box and taken along every day while working in the game reserve. Although the individual animals could later be identified without the aid of the photographs, it was still found handy to write the abovementioned personal history of each animal on a central card system. For instance if a foal showed some particular form of behaviour for the first time, it was easy to check back quickly to determine its age. The date on which the foals left their parental breeding units and other information could be treated similarly. To take these photographs a Nikon F camera with a 200 mm telephoto lens was used.

3.1.3 Observations.

The various study areas were visited as frequently as possible. Most of the time an average of a week or longer each month was spent on the Daan Viljoen Game Reserve. As most of the observations on behaviour were carried out here and the same methods later applied elsewhere, the methods used here will be discussed.

The procedure normally followed consisted of locating a group of zebra as shortly as possible after first light. These animals were then observed from the vehicle at distances that varied from approximately 50 to 200 metres until last light in the evenings. The observer always tried to have a drainage line between himself and the hill or slope occupied by the zebras as this seemed to make them more at ease.

Notes on their activities were jotted down at five-minute intervals. At these times it was noted how many of the group of animals under observation were actually grazing or performing other activities. At half-hour intervals the irritation caused by insects was measured by counting the number of times an animal twitched its tail in one minute. For accuracy a stopwatch and tally counter were used. This was done with three animals selected at random, in a group. Social behaviour was observed and noted throughout the observation period. The various activities were then divided into half-hour time intervals and the percentage of animals performing a certain activity determined. For certain other activities one hour time intervals were used.

3.2 CHARACTERISTICS OF THE HARTMANN ZEBRA SOCIAL SYSTEM.

Of the many factors which may influence the growth of populations, one which has been receiving more and more attention lately is that of social organization. The influence of social organization on species depends upon the existing degree of specialization which varies from species to species and upon the different environmental situations.

Highly organized populations tend to protect species against under-population by promoting survival and against over-population by developing territoriality. On the other hand highly organized populations may have difficulty in reacting to a changing environment and cannot recover so rapidly if the population is reduced to small numbers.

It is through its behaviour that an animal establishes its relations with its environment, including individuals of its own and other species. (Ewer, 1968 and Scott, 1958). Most animals show some degree of social behaviour; thus they must be able to adapt to changes in the social environment. Scott (1958) points out that the growth, limitation and survival of populations are related to the behaviour of its members through social and ecological organization. Equidae have, until recently, received only passing attention from behaviouralists. The first behavioural study on these ungulates was done by Antonius (1937) in which he distinguishes two main types of social organization. In the one type the groups are formed of females and juveniles and are dominated by a single male. This dominant male both directs the movements of the group and defends it. This is a more gregarious type of organization and is characteristic of the true horses, or caballus group. Dobroruka's (1961) study on the Przewalski horse, Equus przewalski, bears this out.

The other type of organization described by Antonius is found with the asses. Here the sexes remain apart for the greater part of the year. The males are solitary or congregate into small groups. The females and juveniles, however, form groups under the leadership of experienced females. It is only during the breeding season that the males join these female groups and try to mate as many as possible of the oestrus females.

Antonius (1937) failed to find any sign of social organization in the Burchell's zebra (Equus burchelli). Klingel (1967) however, found that a very definite social structure exists in the species. According to Klingel there are three types of groups -

(i) Family groups, consisting of an adult male, one or more females and their young. Although the stallion is dominant, the group on the move is usually led by one of the mares, the others following in order of their dominance. The stallion may occasionally lead but more commonly he brings up the rear, or moves parallel to the group. The family group is remarkably stable. The females remain in the same group for their adult lives. The stallion is replaced only when he becomes weakened by old age or sickness.

(ii) Stallion groups, which are formed by young males that leave family groups of their own accord. Within these stallion groups no dominance is shown. Young stallions later establish their own groups by abducting young females from an existing family unit.

(iii) Solitary stallions form the third type of group.

Under certain conditions many of these groups come together to form large concentrations. This is found when grazing conditions improve in a certain area after a rain. No change occurs in the social structure, however, as both the family groups and bachelor groups maintain their coherence.

Ewer (1968) comments that this organization as described by Klingel closely resembles what has been found in many artiodactyls but with this difference: The coherence of the group appears to depend more on mutual ties between the females than upon the herding activity of the male. The result is a greater long-term stability than is usual in artiodactyl harem groups.

The present study shows that basically there is a great similarity in the social organization of *Equus zebra hartmannae* and *Equus burchelli* The basic groups are the same: Family groups and bachelor groups. Although solitary males are known in the Hartmann zebra social system, they do not warrant a group of their own. In a sense they actually represent a form of bachelor group and they only form 3.6 per cent of the total population. Such differences as do exist will be discussed in the following pages.

In the social organization of *Equus burchelli* and *Equus zebra hartmannae* we thus find an exclusive one-male dominance over a given number of females, and a characteristic social hierarchy among the females. In contrast to the "territorial" type of social organization, the "harem" type of organization shows much more adaptability in relation to the nomadic life led by the Hartmann zebra. As shown by the wildebeest (Estes, 1966) the basic territorial social structure has to be modified considerably to facilitate their annual migratory habits.

As already discussed, highly organized populations have some very definite advantages such as survival. No social organization on a population basis could be found in the Hartmann zebra, and Klingel (1967) also reports negatively on the Burchell zebra. However, it was found that the Hartmann zebra population is made up of many sub-groups, highly organized on the social level, comprising family groups and bachelor groups, as discussed above. The advantage of this "sub-group" organization is that it protects the whole population against over-population by spacing the various family groups. It also ensures both an adequate food supply for the females and their foals, and selective breeding.

Another advantage in the social organization of the Hartmann zebra is in the gene flow. Theoretical studies in quantitative genetics show that the structure of a population is very important in governing not only the genetic variability of the population but also the speed with which new adaptive genes may spread. Wright (1950) has shown that the optimal type of population structure is one where the population is divided into semi-isolated breeding units, with a certain amount of inbreeding proceeding with the units joined genetically by a limited amount of migration between populations. The basic social organizations found with Hartmann zebra thus fulfils the prerequisites of obtaining maximum evolutionary benefits.

The social organization and cohesion of the various family groups will be dealt with elsewhere. In general, however, it was found, as discussed by Lorenz (1963), that the social order in family groups is built on personal relationships. The family group is characterized by the fact that it is held together by reactions elicited by one member on another and the attachment reactions are inseparably linked with the individualities of group members. Lorenz (1963) is also of the opinion that the pre~~p~~requisite for every personal bond is a selective habituation to all stimuli emanating from individually known members of the group. This probably also is the precursor in the phylogenetic evolution of social behaviour.

As will be seen, ritualization also plays an important part in the social organization of the Hartmann zebra. Apart from being important in mood transmission in the family group it also has three other very important functions. These functions will be discussed separately and in more detail elsewhere but briefly they are important to -

(i) suppress fighting,

(ii) unify the group through the medium of social hierarchies,

(iii) unite the group as an independent entity against other similar family groups.

The bachelor units are mainly formed by immature males and most of them become sexually mature during the time of their association with the bachelor group. While in this group selective pressure comes to bear - only the more worthy males acquiring their own breeding unit. Bachelor units function thus both as a natural selector for the best males as well as male reservoirs for replacing dominant males that become senile or die.

3.3 THE BREEDING UNIT.

To avoid any possible anthropomorphism, the term "family group" as used until now, will be replaced by the term "breeding unit". The term family group may cause confusion. In a way it is also more applicable to a female and her foal(s) than to the congregation of a male and/or a number of unrelated females and their foals. A breeding unit therefore consists of a dominant male and an adult female or females with or without foals. Sometimes an adult female may be accompanied by two of her foals of different ages.

3.3.1 Composition of sex and age classes in the breeding unit.

This aspect will be more fully dealt with in the chapter on population dynamics. Figure 3.1, based upon the result of 463 observations, gives a clear indication of the number of individuals in various breeding units. Altogether 22,9 per cent of all breeding units consist of five individuals. In 53,9 per cent of the observations the numbers vary between four and six, while 65,2 per cent varies between four and seven. The biggest breeding unit observed consisted of 13 animals (6 per cent) while only 5,2 per cent consisted of two animals. The males on the average had two or three females. The largest observed number of females herded by a single male was six. In his paper on the Hartmann zebra Klingel (1968) found that the average family size was 4,7 with the maximum being 9. The dominant male had an average of 2,2 mares in his family group with the maximum being 4.

In the Burchell zebra, Klingel (1967) reports that the biggest "family" consisted of 16 individuals, with the average being 4,5 to 7,5 - it differs in various populations. The number of females varied from one to six with the average being 2,2 to 2,8.

Fig. 3.1 Distribution of breeding unit sizes for *Equus zebra hartmannae*.

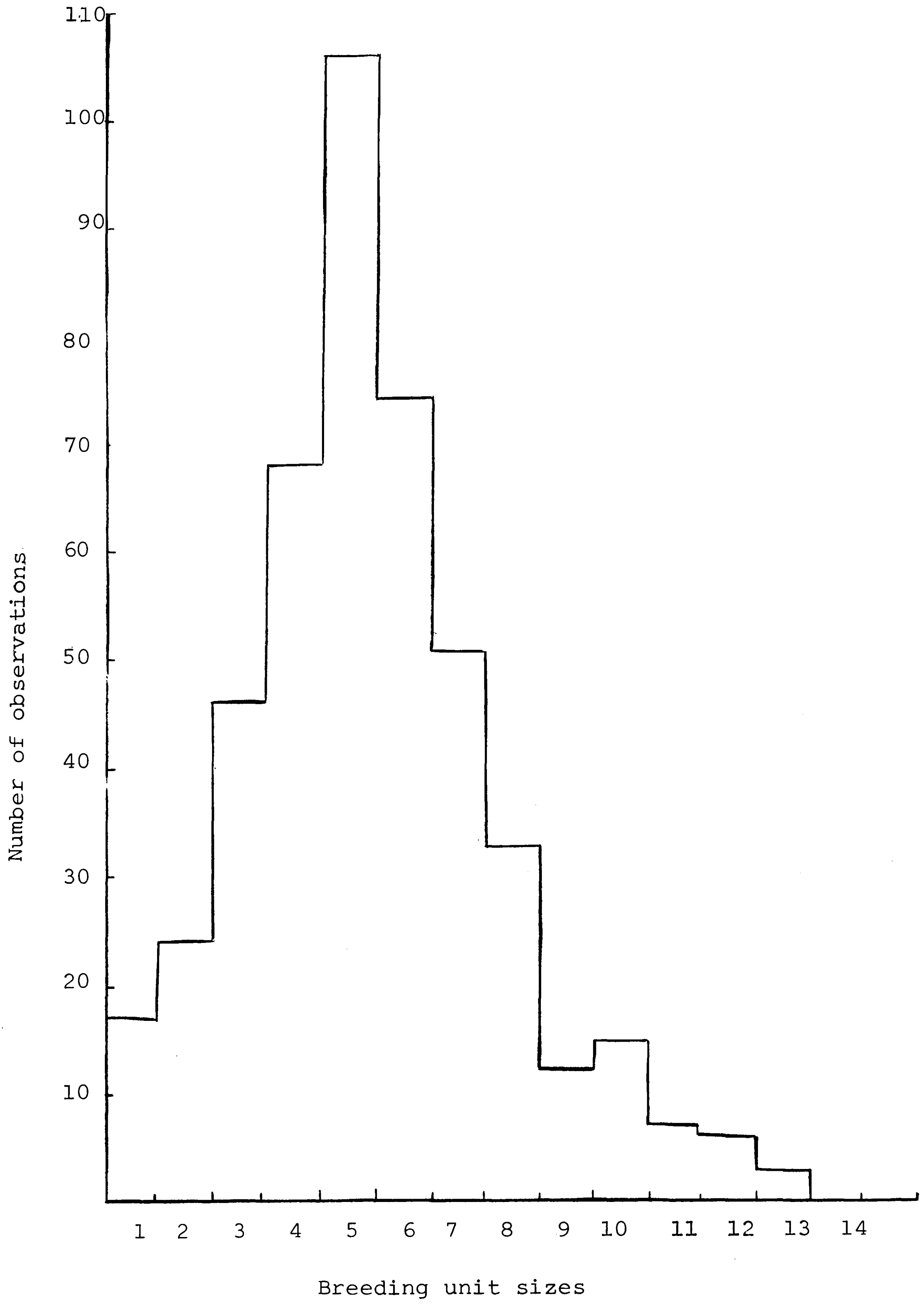


TABLE 3.1

AGE RATIOS OF EQUUS ZEBRA HARTMANNAE.

	Total individuals observed	Adults (males and females)	Foals (up to 2 years)
Daan Viljoen Game Reserve (1970).	48	65,8%	34,2%
Other field study areas.	257	71,9%	28,1%
Mean.		68,8%	31,1%

Klingel gives no indication as to age classes. Field studies on the Hartmann zebra produced the following age distribution, as shown by table 3.1. As can be seen approximately one-third of the population of the breeding units consisted of foals. The higher percentage of foals in the Daan Viljoen Game Reserve is probably due to their higher survival rate in the relative safety of the game reserve. These foals may be divided into two age classes to show the following age composition:

Under 1 year	61%
1 to 2 years	39%

The lower figure in the one to two year age group is due to the fact that a certain number had already left the breeding unit at this stage.

Fifty-two breeding units (the animals at Daan Viljoen Game Reserve excluded) representing 257 adult animals were positively sexed in the field and revealed the following ratio of males to females : 35,2 per cent to 79,7 per cent or a ratio of one male to every 2,26 females.

The male: female ratio at birth is approximately equal as proved by observations at Daan Viljoen Game Reserve as well as a collection of foeti. The adult male : female ratio is similar. (Chapter 4: Population dynamics). It seems therefore that approximately 50 per cent of the males are in bachelor-unit reservoirs.

3.3.2 Social organization.

It is clear from field observations that the breeding unit, formed by an exclusive one-male-dominance over a number of females with their progeny, also forms a social unit. The factors contributing to the social organization in the Hartmann zebra are complicated. Field observations showed that individual variations such as age, size, sex of the individual and the oestrus cycle all play an important part in the establishment of social order. Furthermore it was found that the individual status within the breeding unit varies significantly with the same factors: Age, sex, oestrus condition, physical health and/or weakness.

Several associations can also be defined in a breeding unit. From a survival-of-the-species viewpoint the primary association is between the female and her foal. This association, however, is dynamic and changes with every new foal the female has. A secondary association is that between the various females and the dominant male, whilst a tertiary association can be defined between the various females in the breeding unit. The latter two associations are much more stable and as will be seen, much of the social organization of the Hartmann zebra is based on the persistence of these two associations. All three associations together can be considered the bond in a breeding unit.

The role of the dominant male varies significantly from group to group. It is also possible to differentiate his behaviour in newly formed breeding units from that in old established ones. Within a newly-formed unit, dominance by the male is quickly manifested by aggressive herding of the females and preventing any from straying to other units. During this initial period the dominant male, to ensure maintenance of his group, avoids all contact with other zebra groups. The male maintains discipline during this stage quite adequately by threat behaviour. In these newly formed units a pattern is formed, which is more pronounced in the older units, of a sensitive balancing force that has been achieved through social learning by the individual animals that constitute the unit.

In animals with a territorial social organization, the wildebeest (Estes 1968) for instance, the male protects a piece of ground. With Hartmann zebra the dominant male takes possession of a group of females which he also protects against encroachment from other males. The basic function of these two types of social organizations are the same, even to the psychological advantage of the owner, be it territory or females. When the Hartmann zebra dominance relationship among the females is established, threat episodes become extremely rare. The relationship of the newly established dominant male now also changes in regard to other zebra units in the area. In the Daan Viljoen Game Reserve this was found to happen within the second month after taking over the female(s). The long range alertness to the presence of other groups is relaxed to some degree. When two breeding units graze on converging courses or when they suddenly come within thirty to two hundred metres from each other, the dominant males immediately approach one another. No actual aggression other than threat takes place; it is all ritualized to a high degree and will be discussed elsewhere. The ritual at this stage, apart from the meaning to his opposite number, is probably also directed to his females. It serves as a constant reminder to them of his dominance, by showing his ability to face up to an opponent. This will also be discussed in more detail elsewhere. In the older breeding units the ties between the various females seem to contribute more to the coherence of the unit than the herding done by the male.

As pointed out by Allee (1938) the main duties of communal life in many of the herd mammals are borne by the female. This was also found to be the case with Hartmann zebra in the breeding unit. Once the male has manifested himself in a strongly dominant position, he shows little interest in the social organization within the unit. His role thereafter is mainly directed outwards although he protects the unit when danger threatens, and mates with the females in oestrus. The females rear their young and herd together. One of the females takes the initiative whenever a new activity is to be performed. In addition, the adult females play an important part in maintaining order within the group. One of the factors which may also explain the relative stability of the zebra breeding unit as opposed to the artiodactyls as already discussed, is the tendency of the young to remain associated with the females for a relatively long time. Ewer (1968) discusses this aspect at considerable length and points out that the psychological effects of the prolonged lactation are just as important as the physiological ones, if not more so, and the prolonged suckling period may have been evolved under selective pressures which have little direct connection with nutrition.

Field observations show that young animals stay associated with the mother for periods varying from 14 months to three years for males and from 14 months to life-long for females.

3.3.3 Leadership and hierarchies.

When the present study began on the Hartmann zebra it was difficult to decide exactly what leadership entailed and whom should be considered a leader. Is the animal which takes the lead when starting on a new daily activity the leader ? Or the female which runs away first when danger threatens ? Or the male which plays no conspicuous role in the normal daily social organization of the breeding unit ? Detailed observation revealed that although a hierarchy exists in each breeding unit, consistent leadership among the females is lacking. Scott (1958) and Lorenz (1963) have both warned against confusing leadership with dominance. Scott (1958) found that in sheep no correlation existed between leadership and dominance. This was found to be the case with the zebra females in the breeding unit as well. Any female takes the lead in only as many cases as would be expected by chance. It was also found that the female which first took to flight when danger threatened nearly always happened to be the female with the youngest foal. This could actually be expected as the youngest foal would naturally be the most vulnerable part of the breeding unit, and that it is of important survival value to the species that the young should be protected. It also follows that it is not always the same female in the breeding unit which has the youngest foal.

No satisfactory explanation could be found in animal behaviour literature as to what leadership exactly entails. Available literature from the vast quantity on human leadership, management and authority was also studied. As could be expected no definition regarding leadership in man could be applied to the Hartmann zebra. As to the question whether leadership is instinctive, Bellows (1959) reasons that leadership qualities are learned rather than inborn. An instinct is defined as an inborn pattern of behaviour, which is common to the race or species. Leadership could not be instinctive. Scott (1958) has some interesting discussions on the leader-follower relationship. It was found in the howler monkey (Carpenter 1934) that there is no tendency for one male to take the lead more than the others, and this leader-follower relationship changes from tree to tree. With sheep the oldest female with the largest number of descendants consistently leads the flock. Frazer - Darling (1937) found the same with red deer. The stag rounding up females by force is a far cry from the true leadership shown by an old female for the rest of the year. She gets out ahead of the herd of females and determines the direction of the group while the rest follow without any use of force. In true leader-follower relationships the behaviour concerned is allelomimetic with both animals responding to each other, but to an unequal degree (Scott, 1958).

From the abovementioned and the available literature it would seen that most ethologists agree that an animal which normally initiates an activity or which takes the lead when moving somewhere is the leader, be it male or female. In the social organization of the Hartmann zebra one would therefore find a type of "floating leadership" between the dominant male and the adult females all depending on which initiates an activity or movement. It is felt, however, that this is not true leadership. These various animals are only movement or activity initiaters and not leaders in the true sense of the word.

For the purpose of this study, it was considered necessary to formulate a definition of leadership as applicable to the Hartmann zebra. This was easier said than done. It was found that in the Hartmann zebra the difference between leadership and dominance is so subtle that it can be considered non-existent. The following definition was ultimately decided upon:

> In the Hartmann zebra leadership or dominance is established as soon as a male, owing to the pressure of the species-preserving function of reproduction, subjects a female(s) to his authority, maintains his authority over her (them) and defends her (them) from danger.

When this definition was tested against field observation it was found to hold good. Although the male normally does not show any interest in the social organization within the breeding unit the dominance-subordination relationship is highly developed between the male and the females. This relationship is established as soon as a breeding unit is formed. In the older breeding units the dominant male only seldom inflicted his dominance on the rest of the unit. When he takes the lead they invariably follow him. Only one exeption to this was observed. Quote from field notes:

Daan Viljoen Game Reserve	Date:
Breeding unit 6.	5 April 1970.

" 6.45 p.m. The breeding unit is grazing on a slope approximately 4 kilometres from the dam. Dominant male 6A

> marches away in direction of the dam, apparently on his way to water. Soon realizes that his intention movement is not followed by any of the rest of the unit. He quickly turns around, makes a few threat gestures, herding them and when he again moves away the rest of the breeding unit follow him."

While the dominant male is actively engaged in rituals with a bachelor unit, or in the greeting ceremony with another dominant male the females may graze up close. It was observed on several occasions that he would then break away from his adversary and threaten the females who would then move away. This threat had the tendency to incite the dominant female to a feverish hierarchal activity causing the whole unit to move away at a brisk pace for up to 100 metres. At the risk of being anthropomorphic one wonders whether this is not a case of delegated orders. It was furthermore also found that whenever an alarm was given the male always was the first to investigate. He would also nearly always take up a position between the source of danger and the breeding unit. With the breeding unit moving away he showed a tendency to bring up the rear. The advantage of this behaviour to the survival of the species is clear. It allows the females who are important for breeding purposes a greater margin of safety and should the dominant male be eliminated there is always someone from the reservoir of bachelor males to take his place.

One should be very careful, however, not to underestimate the importance of the male to the breeding unit. Its expression in the above-mentioned situation does not fully show the real importance of the social functions that this animal fulfils. One may briefly list the social functions of the dominant Hartmann zebra male as follows:

(i) By preventing serious fights within the group. When a young female comes into oestrus for the first time, or when a strange female in oestrus is abducted by the male, the other females immediately turn their "wrath" on her. The author is not sure whether this is to force her into a low hierarchal position or to drive her completely from the breeding unit. Both may be true to some extent. In the field this was observed once, when a young female was chased as far as 400 metres. She would always try to get near to the male which, just by his passive presence, apparently offered her enough protection. In this one case where the rest of the females managed to separate her from the male and chased her away, he followed them at a run and she soon managed to gain security again at his side. They copulated several times during the day.

(ii) By taking up a defensive position when his breeding unit is threatened by a predator or other source of danger.

(iii) By threatening or chasing an "alien" of the same species or of a conspecific group. This may also serve to remind the rest of the group of his dominance.

(iv) By taking the initiative in leading the breeding unit although this only happens in approximately one-third of the cases.

(v) By establishing the breeding unit in the first place.

Klingel (1967) does not doubt that the male forms the head of the social organization in _Equus burchelli_, followed by the second in command, the dominant female, and the rest of the females in order of their rank in the social hierarchy. The dominant female starts any movement and indicates direction and speed. She decides on the sleeping place, dust-bathing site, grazing area and where to shelter. The foal has the same status in the social hierarchy as its mother. When the animals move anywhere, the dominant female takes the lead with the rest in order of their dominance. The male has no definite place, but usually follows last or to the one side. The social hierarchy in the females is not stable and may change as quickly as once a month, but in one marked group Klingel observed, the social hierarchy stayed the same for almost a year. He could not determine which factors resulted in this fast change-over, nor what promoted an animal in the hierarchy.

The situation is not exactly the same with the Hartmann zebra. The male is nominally the head of the social organization. A very strict social hierarchy exists among the females but the dominant female cannot be considered the second in command. Any one of the females in the group may initiate a specific movement but she always pays some attention to the behaviour of the rest of the females. It seems that this involves some degree of mutual stimulation. This type of behaviour is called by Scott (1958) allelomimetic behaviour and is defined as behaviour in which two or more animals do the same thing, with some degree of mutual stimulation. A female and her foal have been observed to leave the immediate vicinity of the rest of the breeding unit and start dust-bathing at a point approximately 200 metres away. She was already dust-bathing when the rest of the unit followed her. This particular female was about halfway down the social hierarchy.

With the Hartmann zebra the foal does not seem to have the same status in the unit as the mother. Foals are ignored completely in any activity centred around hierarchy. The hierarchy among females is most noticeable when the unit is dust-bathing or resting in the shade of trees. Females take turns in dust-bathing in strict order of their social status. After all have dust-bathed they usually linger around under the shade of trees. From this stage onwards dust-bathing occurs on a completely random basis. On one occasion a female of lower rank was busy in the dustbowl when a higher-ranking female approached and threatened-chased her a short distance. A foal from a female of still lower rank then approached and used the dustbowl while the higher ranking female was still busy with her other rituals. On another occasion a female and her foal were standing in the shade of a tree. A higher-ranking female moved over, threatened, and the lower-ranking female left the shade of the tree to go and stand 10 metres away in the sun. Her foal remained in the shade, however, both the foal and the higher-ranking female completely ignoring each other.

No specific marching order could be observed in the Hartmann zebra. That the male normally takes up the tail end in any movement was frequently observed. This usually happened because he would be sleeping in the shade of a tree and might only realize that the females were moving away after they had already covered 50 metres or more. He would then follow them in a leisurely way. Once the following observation was made:

> The females were grazing while the male stood in the shade of a tree. When he first realized that the females had gone, they were already over a second ridge, 800 metres away and completely out of sight. He quickly turned around. The females were moving upwind and apparantly having got their scent he set off after them at a brisk trot.

The tendency of the male to move parallel to the breeding unit was also observed; this usually happened so that he could be between his mares and an adversary or the bachelor unit.

During the three years that the Hartmann zebras were kept under observation at the Daan Viljoen Game Reserve no change in the rank of a female in a breeding unit was observed. The social rank, or hierarchy, can be just as stable as the breeding unit itself. The only form of change was observed with the establishment of new hierarchies. This happened when the dominant female (6B) in breeding unit 6 died from natural causes. The second highest female automatically became the dominant female while the rest of the females stayed in the same social order as before. The second observation was during the time that the dominant male 5A was removed from his breeding unit for a month. Female 5D, the lowest ranking female in this breeding unit 5 was "abducted" by a male from a bachelor unit (See details under formation of new breeding units). At the same time this male also managed to attach another young female (5F), also from the breeding unit 5, and was actively herding them. Female 5D who until this stage had completely ignored 5F immediately began threatening her continuously and chasing her about - very obviously establishing for herself a dominant position in the new breeding unit.

3.3.4 The influence of sex on the social organization.

It is difficult to determine exactly to what extent sex influences the social organization of the Hartmann zebra. Females have a gestation period of twelve months and an oestrus period of only two to three days with a dioestrus period of approximately three weeks. Once fertilization has been achieved no sexual behaviour is shown until after the foal is born. Under such conditions, it will be appreciated that the sex relationship in general tends to form a relatively unimportant part of the social organization of the animals, except for the function, for a limited period, in the establishment of new units or the enlargment of existing small ones. This is discussed in greater detail under "formation of new breeding units."

As may be assumed, the oestrus cycle in the virgin female is very important to the whole social structure of the Hartmann zebra. With young females who are undergoing their first oestrus period it means the end of being an "incognito" member of a breeding unit. The females of the unit, as well as the dominant male and other males, immediately begin paying her attention. This first oestrus period for the young female is marked by a high degree of aggression from the females in the group. The hectic period is further marked by the frolics of males trying to abduct her.

The female in gestation has no discernible influence on the social organization of the breeding unit.

3.3.5 Stability of the breeding unit.

The associations between the individual females in a breeding unit are much stronger and more lasting than those between the females and the dominant male. Klingel (1967) came to the same conclusion when he stated that the coherence of the group appears to depend more upon mutual ties between the females than upon herding activity by the male. This association is even stronger than the tie between the females and their progeny. The initial association between mother and foal is very strong but gradually declines as the foal grows more independent. This association between a female and her young may thus become very loose but the ties between the female and her female progeny are apparently never completely broken. This, however, can only begin to have an influence on the already strong cohesion between females in the breeding unit after the female progeny have reached a certain age, and also only in the cases in which they are not abducted beforehand.

The question thus formulated by the above is what factors or stimuli do form and maintain the bond between the adult females in a breeding unit ? This and similar problems, viz., the cohesion in any social group (flock, etc.) have been considered by many workers (Lorenz 1931, Allee 1938, Tinbergen 1951 and 1953, Scott 1958, Barnett & Evans 1965, and Ewer 1968). There is general agreement that the behaviour patterns aimed at limiting aggressive acts, sometimes in ritualized form, lead to the promotion of social cohesion.

One very marked behavioural trait of the Hartmann zebra, the social hierarchy, may lead to the establishment and maintenance of this bond between the adult females of a breeding unit. Initially, of course, no bond exists as females, strange to one another, are forced into a unit by the herding activity of the male. One is amazed, however, at how soon and at what high intensity these strange females set out to establish a social hierarchy. When two strange females in the new breeding unit accost each other for the first time, either actual fighting takes place or one gives way immediately. Normally the female first recruited by the new dominant male has an advantage over the second recruited female. This, however, is not the case when the second female is much older and consequently larger then the first female. This latter situation, however, only rarely arises because of the cohesion between females of existing breeding units and the limited number of times they are abducted by other males. The weaker of the two females quickly retires. During subsequent meetings the non-essential parts of the behaviour pattern are eliminated and the dominant one (or higher ranking female) need only make a threat to cause the subordinate female to move slightly away. Scott (1958) points out that learning connected with fighting behaviour has a tendency to be long-lasting, and the thus established dominance relationship is usually very stable. It is also a behaviour pattern aimed at limiting fighting and thus promotes social cohesion.

Even in old-established breeding units, where the females must have known one another for years, high-intensity activity to affirm social status is striking. Field observation has shown that this activity may occur anything between two to eight times per pair per day (the latter in newly-established breeding units). In a breeding unit with six females theoretically 15 possible pairs of females exist, and this activity can thus theoretically take place 120 times per day. No other single activity takes up so much time and energy in the social organization of the Hartmann zebra. The eliciting threshold of this behaviour is very low and it has become so stereotyped that it can be considered ritualized. This then brings us to another very important function of this ritualized behaviour in the cohesion of adult females in the breeding unit, namely instinctive movement. This is described by

Lorenz (1963:55) as follows:

> "The newly arisen motor co-ordination of the ritualized pattern bears the character of an independent instinctive movement; the eliciting situation, too, which in such cases is largely determined by the answering behaviour of the addressee, acquires all the properties of the drive-relieving end situation, aspired to for its own sake. In other words, the chain of actions that originally served other objective and subjective ends, becomes an end in itself as soon as it has become an automatic rite..........
> The independent instinctive movement is not a by-product, not an "epi-phenomenon" of the bond holding the two animals together; it is itself the bond. The constant repetition of these ceremonies which hold the pair together gives a good measure of the strength of the autonomous drive which sets them in motion."

One may thus assume that the hierarchal behavioural activities shown by the various females of a breeding unit form a chain of cohesion from the highest female in the social order to the lowest.

The striking stability of a breeding unit may also be illustrated with two examples from the Daan Viljoen Game Reserve.

Breeding unit 1.	Date: 18th August, 1969.

Male 1A that has led a solitary life for the last 18 months, has succeeded in taking over breeding unit 4 from 4A. He (Male 1A) is however only interested in two of the four adult females in this breeding unit. He actively herds the two females and a small foal while trying to keep the rest of the animals away. He is very nervous and keeps his new "bounty" constantly on the move and away from all other social units in the area.

After a week he accepts the inevitable and the two sections of old breeding unit 4 join as breeding unit 1.

Breeding unit 5. Date:
January to February 1971.

> On 16 January, dominant male 5A was removed from his breeding unit, both for physiological experimentation and to test the strength of the bond in the breeding units. After 16 days (31 January), a male (2C) from a bachelor unit joined the breeding unit. Eleven days later (11 February) he succeeded in abducting female 5D and her one-month-old foal, and 5F, a young foal in her first oestrus; but the rest of the unit maintained their solidarity. When the male 5A was released six days later (17 February), he immediately rejoined the unit; and two days later female 5D rejoined the group.

It is significant that the cohesion of the social bond between the females in this breeding unit stood up to 27 days without the presence and the possible influence of the male. It is also significant that the only two females that did break away were both in oestrus, and that one returned after the original male came back.

3.3.6 Behaviour patterns between individuals.

3.3.6.1 Individual recognition.

The success of the social hierarchy and even the maintenance of the Hartmann zebra social system depend on the ability of the various members of a breeding unit to differentiate between one another. From field observations it is quite obvious that the social encounters between the different members are based on mutual recognition. Apart from the fact that this must take place through sensory perception, it is not clear exactly how this is achieved. The two senses that seem to be the most important here are olfactory and visual. Of these two, it is the author's belief that visual stimuli are more important in the various Hartmann zebra units. The conspicuous individual markings of the Hartmann zebra greatly aid visual recognition. Klingel (1967) mentions that in the Burchell zebra acoustic characteristics are also important for individual recognition. In the western Etosha National Park, where both the Burchell zebra and the Hartmann zebra occur in the same area, it was observed that the Burchell zebra were much more noisier than the Hartmann zebra. It may thus very well be that this characteristic is also a method for individual recognition. In the Hartmann zebra however, the impression was formed that the sounds emitted were largely of communicational purpose rather than identificational.

3.3.6.2 Ritualized threat and displays.

After the male has established his dominance over the females, most of the social contacts in the breeding unit are between the females. The motivation behind this social contact is mainly to form and maintain a hierarchy.

The primitive or basic mechanism in the establishment of a social hierarchy is aggression. Aggression is defined by Lorenz (1963) as the fighting instinct in animals which is directed against members of the same species. That intra-specific aggression has a survival value for species is certain, but it is just as important that in a breeding unit it must be inhibited. The usual assumption is that displays and threats drive others away without the need for harmful assault. Ewer (1968: 154) defines a threat as a signal denoting that, contingent upon some act or failure to act on the part of the recipient of the signal, hostile actions will be taken. Ewer also points out that threat frequently includes actions which serve to draw attention to threatener's size or weapons; such preliminaries are then referred to as an intimidation display. In the Hartmann zebra this consists of the aggressor baring its teeth.

Apart from the development of hierarchy (and thus contributing to the stability of the breeding unit) threat may also be used by the females in defense of their young. On the 28th October 1970 a female was standing in a rest posture with her foal lying next to her. Two other foals were engaged in play, their activity bringing them closer and closer to the small foal lying on the ground. When the danger of their tramping on him became imminent the mare, without moving, displayed a threat posture. The two playing foals immediately moved away. Females also use threat displays to expel young adults from the breeding unit and also to repel animals from other units. It was observed in the field that it is even used inter-specifically by driving kudu from under shade trees and on one occasion a gemsbok from a feeding trough.

As in most animal species threat behaviour has also been ritualized. According to Lorenz (1963:72) ritualization is the phylogenetic process which creates a new autonomous instinct which interferes as an independent force with all other instinctive motivations. The primary function of ritualized threat consists of communication to prevent the harmful effects of aggression by inducing mutual understanding between members of a species. Ewer (1968:19) takes the same standpoint and stresses the fact that if it is advantageous for a quick and correct response to be made, then there will be selection for making the signal more obvious and unmistakable. In the Hartmann zebra ritualized threat behaviour consists of the following:

> The ears are pulled back tightly against the head, the head is lowered and the neck stretched forward as far as possible and the teeth are bared. The tail is lashed and the animal charges a couple of metres.

During threat display no contact is ever made between the two participants. The animal at which the threat is directed sometimes begins moving off immediately at the first sign of this display. This quick reaction to the threat display sometimes results in the latter part of the display, viz. the short charge, not being carried out. One is impressed by the passive acceptance by the lower ranking females of this threat behaviour. No very marked submissive behaviour, as is for instance shown by the wolf (Schenkel 1967) and various species of gazelle (Walther 1966) was ever noticed in the Hartmann zebra, apart from the quick moving away of the lower ranking female. This submissive gesture of moving away by the lower ranking female is normally accompanied by a laying back of the ears, but not as tightly against the head as in the animal carrying out the threat display and the head is held high in contrast to the lowered head in the threat display. The tail in the lower ranking female is lifted above the horizontal line formed by the back and rump and held rigidly backwards.

3.3.6.3 Behaviour between dominant male and females.

The maintenance needs of the breeding units do not necessitate any other contact, apart from ritualized threat between the adult females and it seems that contact is simply avoided. Social contact in the way of amicable behaviour, however, occurs between the females and the dominant male. That this pattern of amicable behaviour plays an important role in the maintenance of social cohesion is also discussed by Lorenz and Ewer (1968). According to Lorenz (1963:148) amicable behaviour should not be regarded as merely the expression of an independently existing bond between the animals concerned. He maintains that once an innate amicable pattern has been evolved, this will show the properties characteristic of built-in forms of behaviour with an increasing need to be performed the longer it is denied outlet. A social companion provides the only adequate means of discharging the pattern: thus the situation is reached when the need to show friendly behaviour is greater than just to have a social companion. It thus forms a bond between individuals.

During field observations it was observed that each of the females would at least once a day make contact with the dominant male. This sometimes consisted of naso-nasal contact, but mostly the female would rub her shoulder against the male while moving past him. This amicable contact in the Hartmann zebra is always of a very brief duration. Klingel (1967) found that in the Burchell zebra the dominant male showed preference for a certain female in the breeding unit and that this female was not necessarily the "leader" female. No such favouritism or preference for any one female in a breeding unit was ever shown by a dominant male in the Hartmann zebra. Occasionally a higher ranking female chased a lower ranking female from the male, but this occurred only rarely.

When male 5A was removed from breeding unit 5 for a period of one month for experimental purposes, an interesting observation was made. During the first three days the rest of the breeding unit definitely searched for the male, roaming all over the Daan Viljoen Game Reserve. Every other breeding unit encountered was accosted. They would first look at the other unit from a distance and then move in. They would intermingle with the other breeding unit, and various females would make naso-nasal contact, then swiftly whirl around and kick out. Even the most lowly-ranked female of breeding unit 5 showed this very aggressive behaviour. All this took place at a very fast pace and in a relatively short time. One of the author's most memorable sights occurred during this period. He was watching another breeding unit early one morning, when he first noticed a head appearing over the top of a ridge, looking down onto the breeding unit he was watching. One after another the rest of the adult female's heads appeared next to one another. They all stood looking down at the other breeding unit with ears cocked. It was only when they started running down towards the other breeding unit that he identified them positively as breeding unit 5.

After about a week breeding unit 5 seemed to accept the inevitable and although they still roamed around they no longer accosted any of the other breeding units.

3.3.6.4 Behaviour between adults and foals:

The behaviour of adults in a breeding unit towards its young foals may be subdivided into three categories:

(i) between a female and her own progeny;

(ii) between a female and the progeny of other females; and

(iii) between the dominant male and the foals.

3.3.6.4.1 Between the female and her own progeny.

The behaviour of the female towards her own young foals will also be discussed under Parental Care. The eliciting threshold for maternal behaviour is at its lowest the moment the foal is born (due to hormones and other releasers caused by the appearance and behaviour of the foal). By grooming and other amicable behaviour the foal instinctively tries to keep this threshold for maternal behaviour as low as possible. However, despite this, the maternal behaviour in the female declines while the eliciting threshold for the "expelling the foal" behaviour becomes lower. Exactly what innate mechanism causes this to happen is not clear; it may have some connection with the hormonal state of the mother and the drying up of the maternal milk supply. The change in behaviour of the female towards her foal is already noticeable when the foal reaches an age of approximately 10 months and is weaned. A more dramatic change, however, takes place three to six months later, shortly before the birth of the new foal. At this stage the female tries her best to drive the foal, which is now approximately 13 to 16 months old, out of the breeding unit. This behaviour may last as long as a month and at the birth of the new foal it shows another change. Once the new foal is born, the mother completely ignores the older foal if it has not already left the breeding unit at this stage. Although the older foal still follows the mother with her new foal, social contact virtually ceases until the foal either leaves the breeding unit or (in the case of a female foal) is integrated into the breeding unit by the dominant male. This latter however, only happens infrequently.

Klingel (1967) found that with the Burchell zebra the female foals disappeared from their breeding unit at an age of between one to two years, the average age being one and a half years. According to his observations it appears that the female foals usually leave the breeding unit of their own accord although they are sometimes driven out. More generally, however, they are abducted against the will of the dominant male by other strange males. The male foals in the Burchell zebra leave the breeding unit at an age of one to two years. This behaviour in the male foals is voluntary and Klingel emphatically states that they are not driven out by the adult male or female.

In the Hartmann zebra it was found that no difference existed in the behaviour of the female towards her progeny-.male or female. The "expelling the foal" behaviour was directed by the mother with as much vigour against female foals as it was against male foals. From observations at the Daan Viljoen Game Reserve it was found that approximately a third of the foals leave the breeding unit at the age of 14 to 16 months as a direct result of this behaviour. The ratio of newborn foals to foals older than one year is approximately 60 : 40 From the age of 14 to 16 months the foals (male and female alike) leave the breeding units voluntarily so that only 8 per cent of a breeding unit is formed by foals older than two years. It seems that the age at which the foals leave their breeding units closely correlates with what Klingel found in the Burchell zebra. Furthermore, as all these foals are still sexually immature, it seems that sexual motivation does not play a role in this behaviour.

3.3.6.4.2 Between the female and other foals.

The behaviour of females towards foals of other females in the breeding unit is one of indifference, but while the foals are still young, tolerance. This is especially the case when young foals sometimes amble up for naso-nasal contact with other females in the breeding unit. Females never try to expel foals of other females from the breeding unit, except when the female foals come into oestrus for the first time.

3.3.6.4.3 Between the dominant male and the foals.

The behaviour of the dominant male towards the foals in his breeding unit is also one of tolerance although they are normally completely ignored. In the Etosha National Park the auther once observed a dominant Burchell zebra male trying to kill a new-born foal. The female actively protected the foal by rushing in between the male and the foal. Once while the foal was lying flat on the ground the male reared on its hind feet, but before he could crash down on the foal, the female knocked him to the one side with her shoulder. This behaviour has also been recorded for horses(Pers. com. P. Starke). Behind the Legislative Assembly Buildings in Windhoek a female and male Hartmann zebra were kept in a small enclosure with a number of other game. When the female gave birth to a small foal the male became quite aggressive and after trying to kill his own foal, killed a duiker and another small antelope. He then had to be removed from the enclosure. Nothing similar was ever observed in any of the study areas and the author would rather not hazard a guess at what triggers this killing behaviour in Burchell zebra, horses and in the one instance, Hartmann zebra.

Normally the dominant male only becomes aggressive to male foals older than two years and only when one of the females in the breeding unit is in oestrus. But even then this behaviour does not reach the high intensity of the "expelling of the foal" behaviour showed by females. Immediately after threatening the male foal they may graze again within two metres of one another. On one occasion a male foal (approximately 10 months old) was observed actually hampering the mating behaviour of the dominant male without the latter retaliating.

Quote from field notes:

Daan Viljoen Game Reserve. Date:
Breeding unit 3. 27th October, 1970.

"5.15 p.m The oestrus female approaches dominant male and then urinates. The male sniffs and goes through the flehmen sequence. Her male foal comes running from over 50 metres away, also sniffs and shows flehmen. While doing this he tries to push the dominant male away with the posterior part of his body. After a while he starts grazing and moves away while the male continues with his flehmen activities. After some time the male

5.20 p.m walks over to the female who presents herself. Following the usual preliminaries he mounts but does not copulate. The foal approaches and tries to push the male from the female, bites (groom ?) the male in the side.
The male dismounts and completely ignores the activities of the foal."

Considerable variation was observed in the behaviour of the dominant male towards the female foals. When female foals leave the breeding unit the male does not try to stop them. The female foal that leaves a breeding unit sometimes, for a short period joins up with a bachelor unit or wanders around singly. Klingel (1967) did not observe this with the Burchell zebra. The wandering female foal is quickly picked up by a male which has had sexual experience, normally a male which has lost its own breeding unit to another male or a male with a small (one to two females) breeding unit. Thus a new breeding unit might be formed with these foals which are not yet sexually mature.

Female foals which stay with the breeding unit are normally faced with agonistic behaviour from the older females when they have their first oestrus period. This agonistic behaviour by the adult females may be either to force the young in-oestrus female into a low hierarchal rank or to drive her from the breeding unit. They are now abducted with relative ease by other males. The dominant male will occasionally try to herd or actively defend such a female foal. It seems that the threshold for herding behaviour in the dominant male is raised with each female he acquires, until he no longer actively recruits females for the breeding unit. This is understandable, or else it would defy the whole concept of the social organization evolved by the Hartmann zebra.

This behaviour was once beautifully illustrated at the Daan Viljoen Game Reserve. A female foal joined a bachelor unit and shortly afterwards came into oestrus. Not one of the male foals in the breeding unit was sexually mature enough at this stage to mate with her. One of the dominant males of another breeding unit mated with her several times, with the bachelor unit milling around them and his own breeding unit grazing a short distance away. He never tried herding her to his breeding unit. After her oestrus period passed he joined up again with his own breeding unit while she stayed with the bachelor unit. She eventually formed a breeding unit with another female foal (who at this stage had not yet had an oestrus) and an adult male who was introduced into the Reserve.

3.3.7 Communication.

The social relationship in the Hartmann zebra is based on the prerequisite that an effective communication system exists between the various individuals and between groups of individuals. The mechanisms of communication are either through visual signs (behaviour) and/or through vocalized signals. In the Hartmann zebra the former is probably more important for the social organization on the social unit level. Sounds are normally used to warn other individuals when danger threatens. Tinbergen (1953:81), quoting Lorenz, points out that colours, shapes, calls and movements by one individual have as their only function the release of fitting responses in another individual (of the same species normally). Lorenz (as quoted by Tinbergen) describes this concept as follows:

> "The means evolved for the sending out of key stimuli may lie in a bodily character, as in special colour design or structure, or in an instinctive action, such as posturing, "dancing" and the like. In most cases they are to be found in both, that is, in some instinctive acts which display colour schemes or structures that were evolved exclusively for this end. All such devices for the issuing of releasing stimuli, I have termed releasers (Auslöser), regardless of whether the releasing factor be optical or acoustical, whether an act, a structure or a colour."

As already said, field work on the Hartmann zebra indicated that the principle of releasers seems to be important in the social co-operation of this animal, especially on the social unit level.

3.3.7.1 Communication between individuals of a breeding unit.

Various releasers are used in the breeding unit between the dominant male and adult females, between the adult females and between the foals themselves. Releasers between female and foal will be discussed separately. The most important releaser between the dominant male and the females is the herding activity. The releaser for amicable behaviour between male and female is the way a female will rub her shoulder on the flank of a male while moving past. Between adult females there is even a greater range of signals. The way their ears are moved, the angle at which the head and neck are held as well as the movement of the tail are all behavioural patterns which stimulate other adult females. Foals also use releasers to initiate play. This may consist of one racing past another inviting a chase, or it may nibble at the other's knees to start play-fighting. It is clear from the above that all this conveys information on the emotional state of the individual and thus is of communicational value.

Not all communication is based on behavioural releasers, however, as the Hartmann zebra also has a limited number of vocal releasers. Klingel (1967) describes a number of sounds emitted by the Burchell zebra and their meaning. According to him contact with the group is maintained by means of sounds, especially on dark nights. Foals also call their mothers when they become separated. In the Hartmann zebra the following limited vocabulary was found to be used by the animals. Though some of the sounds are frequently repeated, there is little variation in the pattern:

(i) Sign of contentment:- This sound is achieved by forcing the air through closed lips, causing them to slap against each other. This can be considered to be a signal of contentment and is usually emitted whilst grazing or resting.

(ii) Challenge call:- This is a sudden, short, explosive snort, with the qualities of a sneeze. It is relatively loud. This sound is normally emitted whenever something suspicious or strange is seen by any animal in the social unit. It immediately causes the other animals in the unit to be on their guard and all of them will then intently watch to ascertain the cause of the alarm in the first place. In a breeding unit the dominant male will then advance a few feet and again and again utter this sound. This sound is never directed at any other individual of the same species and can be considered as socially negative. The function of this sudden explosive noise might be to evoke a reaction in the original cause of the alarm so that they (the Hartmann zebra) may decide which action, if any, must be taken. During the study the author tried on several occasions to creep up to a social unit to take photographs. When one of the animals emitted this sound it was normally a sign that the author was spotted. If he kept perfectly still the animals would sometimes approach as much as 50 metres while snorting at intervals. As soon as he moved again or stood up they would be gone like a flash.

(iii) Alarm call:- This sound was normally uttered by a unit as they ran away from danger - especially at night. This sound is repeated for several seconds at a time and carries very far. In the Burchell zebra one finds a comparable sound but it is used with greater regularity than in Hartmann zebra. In both cases it warns other groups of animals in the area and often one can hear it being taken up by other groups or units as well.

(iv) Submissive call:- This sound is very highly pitched, and although it is not loud it can be heard over relatively long distances. This sound is emitted by so large a variety of individuals under variable circumstances that it is quite possible that what a human ear registers as one definite call may in actual fact be several. It is mostly heard in the bachelor unit, especially when a dominant male of a breeding unit is in attendance. It is also sometimes emitted by the female during the courtship ritual, probably to confirm her submissiveness. During the "expelling of the foal" behaviour by the female, the foal against whom this behaviour is directed, might also emit this submissive call.

Another type of communication which is found in the Hartmann zebra, but which is more vague, is mood transmission. Mood transmission is brought about or communicated by what may be termed expression movements. This normally happens when an individual starts on a certain behavioural activity - feeding, rolling or defaecation - and the rest of the social unit follows suit. These expression movements, however, all have different inciting thresholds. Activities centred around daily living requirements such as feeding normally have a higher threshold than activities that might indicate danger. When an animal starts on a normal daily activity the rest of the social unit may or may not be induced to do the same. Even if they are so induced, the change occurs at a leisurely pace. Should, however, one of the animals signal an alarm, all of the social unit immediately pay attention. Likewise the threshold for running is much lower than that for walking. The latter has been observed often in the field. A number of social units might be grazing within sight of each other. If one of the units starts moving off slowly, not one of the other social units will pay it any attention. However, should one of the social units start running in a determined manner, it will quickly cause a stampede. Field observations also indicate that expression movements initiated by the dominant male have a lower threshold than any started by the females. Likewise, the threshold for activities started by a female high in the social hierarchy is lower than the threshold of females lower on the hierarchy scale.

3.3.7.2 Communication between mare and foal.

In contrast to the Burchell zebra the foals of the Hartmann zebra were never heard to make a call of their own. One of the more conspicuous releaser signals in the mare-foal relationship is when the foal wants to feed. The foal approaches the female and walks in under her neck, rubbing its side against her chest. If the female is moving forward this behaviour forces her to come to a standstill. The foal then continues with this "crossing of the bows" movement and ends up head to tail alongside the female and starts suckling. During the study period this movement by the foal was initiated 49 per cent of cases from the right hand side and in 36 per cent from the left side of the female. In 15 per cent of the cases the foal tried suckling from behind between the hindlegs of the female. This was invariably unsuccessful, while the percentage of success with the former two approaches was quite high.

Two other types of visual releasers also occur between mare and foal. They are both threat orientated and very much ritualized. The one occurs when the female starts weaning the foal. Although the foal may still try to use the releaser signal discussed above, it becomes less and less successful. At this stage they attempt stealing up to the female from behind. She invariably notices them and goes through the same motions as described earlier, viz. laying back the ears, lowering the head but instead of moving forward she moves backwards in little jumps, picking up both hindfeet a few inches from the ground as though ready to kick out, although she never does. This results in the foal immediately moving away.

The other releaser signal is the same threat display used by adult females in the maintenance of hierarchy, but here it is used to drive the foal out of the breeding unit. The reaction of the foal to this behaviour is learned and not innate as one would expect. This became quite clear from field observations, for when the female first starts this behaviour she actually has to bite to get any reaction from the foal. The foal however, quickly learns to avoid the female when she threat-displays.

3.3.7.3 Communication between different breeding units.

In the social organization of the Hartmann zebra no need has evolved for contact between different breeding units - apart from that between dominant males. The latter however, will be discussed under a separate heading. Social contact between adult females of various breeding units is simply avoided. No need for communication has therefore been developed. Even when, for various reasons different breeding units should aggregate or intermingle, the various breeding units maintain their high degree of solidarity. As mentioned earlier it is only the warning call from one social unit which has any marked effect on other Hartmann zebra units.

3.3.8 Mating behaviour.

The mating behaviour in the Hartmann zebra is relatively simple. As the dominant male and the females in the breeding unit are known to one another, courtship is peaceful with no elaborate ritualization. In the Burchell zebra Klingel (1967) does not describe any mating behaviour apart from the fact that the oestrus female is constantly followed around by the male. Although, as has already been said, the mating behaviour in the Hartmann zebra is simple, it may still be divided into three clear phases:

1. Urination-flehmen sequence.
2. Courtship.
3. Copulation.

3.3.8.1 Urination-flehmen sequence.

The coming-into-oestrus of a female is first signalled by the behaviour of the male. He suddenly starts paying more attention to that female especially when she urinates, which is now more frequent than is normal. At this stage he frequently exhibits flehmen behaviour as well as the tendency to urinate on the same spot as the female. Flehmen is apparently almost universal in the animal world and has been reported in Carnivora and Chiroptera (Schneider, 1930), Bovidae and

Camelidae (Ewer, 1968) and in Equidae.

In the Hartmann zebra this behaviour consists of an individual normally the dominant male, sniffing at the urine of a female in oestrus. The head is then raised, turned sideways with the nose pointing upwards, the lips turned back and the nose wrinkled. As Ewer (1968) points out, the facial expression is rather suggestive of disgust. Apart from the wildebeest (Connochaetes taurinus), where this behaviour is striking in the challenge ritual activities (Estes, 1968), it is normally done in connection with sexual behaviour. In the Hartmann zebra flehmen was also noticed in the bachelor units. Both Ewer (1968) and Estes (1968) are emphatic that this behaviour is not a display. Knappe (1964), as quoted by Ewer, points out that it is a muscular contraction that opens the ductus incisivus that ensures scent molecules to reach Jacobson's organ for olfactory analysis. In the Hartmann zebra it was observed that not only the male showed flehmen behaviour, but females sometimes do the same. On one occasion a female, after sniffing at a spot where an oestrus female had urinated, showed flehmen behaviour which was immediately copied by her three-months old foal.

At this stage, before mating, the flehmen behaviour is not followed by any other sexual behaviour. The male, however, shows a tendency to urinate at the same place as the female. The simplest hypothesis to explain this "marking" behaviour by the male would be that he is covering her urine with his own to indicate to rivals, that might come along, that the female in oestrus is already accompanied by a dominant male. On one occasion after flehmen behaviour, a male was observed to urinate on the spot. He then continued to graze and about half an hour later came across the same place (it is difficult to say whether this happened on purpose or by chance). He stood sniffing at the same place, then pawed the area with his front hoof, sniffed again and showed flehmen.

3.3.8.2 Courtship.

In the Burchell zebra Klingel (1967), as has already been mentioned, does not describe any courtship behaviour apart from the fact that the female is constantly followed by the male. In the Hartmann zebra two types of courtship behaviour were observed. The first type was the most common and was noticed every time that a female was in oestrus. The second type of behaviour was observed on very few occasions; perhaps it is not part of the general courtship behaviour, or perhaps it only occurs at a certain stage during courtship.

In the more common form of courtship displayed by the Hartmann zebra, the male and female sometime graze anything up to 50 metres apart from where the female then approaches the male. In contrast to the behaviour in the Burchell zebra the female approaches the male. Without any naso-nasal contact or any other ceremony she presents the posterior part of her body to the male. The male would then sniff at her vulva and rub the front part of his head (face) against her genital area. This procedure increases in intensity as the female approaches the peak of her oestrus period. When the female presents herself at that stage, she makes little jumps with the posterior part of the body, lifting both hindfeet simultaneously a few inches above the ground. By doing this she rubs her vulva against the head of the male. The male answers by returning the rubbing and then lays his head on her rump. Walther (1958) regards this placement of the male's head on the female's rump as a ritualised intention mounting movement. By doing this the male is signalling to the female his intention of mounting and if she is ready she assumes the mating posture. Walther mentions that this behaviour is found in most of the Tragelaphinae and to a certain extent in Antilopinae. It is also described by Short (1966) for the African elephant, although he does not mention the ritualised function of this behaviour.

The second type of courtship behaviour seemed to be more ritualised.

Quote from field notes:

Daan Viljoen Game Reserve. Date:
Breeding unit 5. 27th October, 1970.

"5.15 p.m All the members of breeding unit 5 are grazing. The female in oestrus and the dominant male (5A) are grazing approximately 30 yards apart. The female starts moving in the direction of the male with head held low and ears laid back. The male picks up his head and with head held high trots closer with an almost stiff-legged gait. When they are 10 yards apart the female stops, emits the submissive call and urinates. The male moves closer and after sniffing at the spot where she urinated goes through the flehmen behaviour. This lasts for several minutes while the female continues to graze and move away. The male continues to smell and rub his nose over the area where the female urinated and again goes through the flehmen behaviour.

5.20 p.m The male moves over to the female who presents herself."

Although he mounted her after the preliminaries they did not copulate - it did not appear as though he really tried. It is difficult to decide whether this behaviour is a deviation from the normal mating behaviour or whether it is an integral part of the courtship behaviour.

3.3.8.3 Copulation.

The ritual where the male lays his head on the female's rump normally lasts several seconds before the male attemps to mount.

During intromission the male lays his head, with ears laid back, between the female's shoulder blades while he clamps her with his front legs. The female lowers her head with her ears also laid back and with lips pulled back. This facial expression in the Burchell zebra female has been called "rossigkeitsgesicht". Copulation normally lasts only a few seconds but is repeated almost at hourly intervals for a couple of days.

3.3.9 Parental care.

In the social structure of the Hartmann zebra the female is alone responsible for the care of the foal. The relationship between the female and foal is dynamic and changes constantly as the foal grows older. With the change in relationship there is also a change in the behaviour of both animals. All this indicates that an innate mechanism exists to make this mutual adaptation between the two members of the relationship possible.

Although no actual birth of foals was seen during the study, preparturitional behaviour was observed on several occasions. As parturition becomes imminent the behaviour of a female to her previous foal becomes changed. During February 1971 female 4B was noticed to be extremely hostile towards her 14 months-old female foal. This behaviour was kept up for two days. Early on the third morning a newly born foal was observed with 4B. A reversal in her behaviour seemed to have occurred towards the older foal. This foal was now once more accepted (or ignored) and allowed to come near to its mother.

External stimuli seem to play an important role in the initiation of maternal behaviour. This seems to be confirmed by the difference in appearance of the newly born and their parents. Tinbergen (1953:209) quotes Lorenz to the effect that this external stimulus serves as an innate releasing mechanism for maternal behaviour in the female. The appearance of the young Hartmann zebra foal viz. the relatively shorter face, lighter colour of the stripes, the long hair covering the body, giving it a woolly appearance, might all be visual, and the latter also tactile, stimuli for this innate releasing mechanism in the female. Apart from the development of maternal behaviour another marked activity of the female during these first few hours is the attention given to the young by smelling and licking, especially the anogenital region. Ewer (1968) suggests that the primary factor involved is the subsequent recognition by the female of its young by its olfactory characteristics. As the foal grows more independent and moves further from the female, recognition is made visually, at a distance but this is always repeatedly confirmed by direct contact. The same is true of the foal in recognizing its mother. Klingel (1967) reports the same for the Burchell zebra.

One of the adaptations in the social behaviour of the female is the need to defend the young foal. During the first three months after the birth of the foal the female is a symbol of nervous watchfulness. At the least sign of danger she is normally the first one of the breeding unit to be off. This behaviour has a definite survival value for the species, as has already been discussed. Yet on several occasions females with newly-born foals were seen to act differently, as though ignoring the apparent survival value for the species. After the birth of the foal they would not rejoin the breeding unit but roam about on their own. Whereas a breeding unit is comparatively sedentary while grazing, this mother with her newly-born female foal would cover at least three times the distance covered by the breeding unit per day. One female, which normally was quite tame, when she had foaled would not let the author's vehicle approach more closely than 300 metres before she was off. After anything from three to ten days these females would rejoin their breeding units. Could it be that the hyper-sensitive watchfulness and protection offered to the foal during the first few days, would not even tolerate the nearness of the other members of the breeding unit ? In all instances where this behaviour was shown by females, they normally rejoined the breeding unit they had temporarily left.

Although Klingel (1967) reports grooming behaviour by the female towards her young foal, no such behaviour has been observed in the Hartmann zebra. During the first few hours after birth, licking of the foal was observed, but thereafter the female did not groom the foal in any way. While the foal is sucking, the female may spend the entire time sniffing at the anogenital region of the foal. Amicable behaviour between the female and foal, however, occurs regularly. This behaviour is usually induced first by the foal. It no doubt serves to promote the maternal instinct in the female and also as a mechanism inhibiting aggressive behaviour in the female (possibly in other adult animals in the breeding unit as well), thus serving to establish a tie between the two.

The amicable behaviour normally consists of naso-nasal contact. Sometimes while the foal is sucking, the female will rub her forehead against the side of the foal. On 28th May, 1970, breeding unit 3 was under observation. Female 3D had a small foal. She sniffed at its anogenital region and then rubbed this region with her forehead, and then the sides of the foal.

Amicable behaviour by the foal is normally directed at the female when the latter is not busy with another activity. The following is a typical example, Quote from field notes:

Daan Viljoen Game Reserve. Date:
Breeding unit 5, 26th November, 1969.

"9.30 am. All the animals in breeding unit 5 are now resting - mostly in the shade. Young foal 5/BB is very active, rubs himself against female 5B, then does a naso-nasal contact for several seconds, rubs his forehead against her sides and rump, stands on his hindlegs and tries to nibble at her neck."

This grooming (nibbling)behaviour was also observed on several other occasions. Normally it was directed at the neck of the female. The female very stoically and patiently accepts any attemps of the foal to play with her. The foal will normally try to induce playing by biting at her knees or racing past her.

Another essential inter-action between the female and foal is the sucking behaviour. The releaser used by the foal to initiate this behaviour has already been discussed. Sucking occurs with both foal and female standing. As with most mammals the young foal also has a behaviour pattern to stimulate milk flow. This takes the form of butting the snout or head against the udder. This butting behaviour is, however, not so violent as has been observed in calves of domestic cows. Both teats are sucked, one at a time, every time the foal feeds. As the foal grows older the butting behaviour becomes more marked. This is probably due to the fact that the female progressively produces less milk and as the foals grow bigger their appetite for maternal milk probably increases. This is emphasized by the fact that they have to be forcibly weaned by the female when they become older.

In the Hartmann zebra a new-born foal was observed to start grazing from the third day. Despite this, as has already been mentioned, the foal continued to suck until it was approximately 10 months old. The foal therefore received, for this period, nutrition from its mother as well as feeding on its own. The frequency with which sucking took place however, was observed to decline fast, especially after the first two months. The newly-born foal sucks once every 50 to 70 minutes during daylight hours. At this stage sucking lasted approximately 50 to 75 seconds, followed by a period of five to 15 seconds during which the foal rested. Then it will suck again for five to a maximum of 15 seconds. The regularity with which the foals sucks declines gradually to twice daily, at which time the female would start her "weaning of the foal" behaviour.

The number of times a foal sucks, as well as the duration of this sucking, declines rapidly from the age of approximately two months. It appears that although the young might be able to survive without maternal milk from an early stage, lactation is drawn out over a longer period than is probably necessary. This may be due to the fact that the actual execution of the feeding behaviour is of more advantage to the species than the nutritional value of the milk consumed. Talbot and Talbot (1963) found that wildebeest calves suck until they are replaced by the next young - approximately a year later. Ewer (1968) discusses the behavioural consequences of slow transition to fully independent feeding, despite the advanced state in which the young of most precocial ungulates are born. Ewer concludes that the primary function of this association might be to keep the youngster under the mother's protective vigilant care, rather than to supply it with food. As mentioned earlier it might also have a psychological effect on the young in regard to their adaptability to the social organization in later life.

The foal will often stand in the female's shade while the latter is grazing or in her lee when an unpleasantly cold wind is blowing.

3.3.10 Foals.

A Hartmann zebra foal is regarded as any young animal from newly-born to the first time it has oestrus if it is a female(s) or until it joins a bachelor unit in the case of males.

The Hartmann zebra foal can follow its mother with relative ease after the first day. Naturally it does not have as much stamina or speed as the adult animals;, this is probably one of the reasons why the female with a young foal will always start moving off first. During the first week the foal stays in close attendance with the mother, often lying down , As the foal grows older it becomes less dependent on the immediate presence of the mother and moves around on its own. For the first six months however, it never leaves its mother for distances of over approximately 50 metres, even when playing with other foals.

3.3.10.1 Play.

Playing is one of the characteristic behaviour patterns of foals. Klingel (1967) reports the same for the Burchell zebra. Ewer (1968:288) maintains that play has four characteristics:

(i) that the motivation is not of that in the "in earnest" situation, for example play-fighting as opposed to real fighting.

(ii) that although it is not performed in a clear order and without relation to an objective, the actions are still orientated.

(iii) that although the same instinctive movements as those of the "in earnest" situation are used in play, they are often exaggerated.

(iv) that play in young animals generally occurs as a regular part of the daily routine.

All four characteristics mentioned above are applicable to the Hartmann zebra, where play behaviour could be d~~e~~ivided into three categories or games:

(i) Racing or chasing games. This is normally the first play behaviour shown by young foals. At first it is played solitarily, but as they grow older they start looking up other foals. From this stage the other two types of games are played: the greeting game and play-fighting.

(ii) The greeting game is brief and consists mainly of naso-nasal contact followed by rubbing of the head against the other foal's rump. This is a direct copy of the greeting behaviour of the older animals. If it were not for the fact that this behaviour was usually executed after the foals had been playing some time it could be interpreted as real greeting.

(iii) Play-fighting is also an exaggerated imitation of the serious fighting. They bite at each others knees, rear up on their hind feet, bite playfully at the mane of the other, trying to force him/her down on his/her knees. This is followed by a continuous whirling movement as they jockey for a better position.

As they grow older the greeting and play-fighting become more pronounced while the racing games are seldom seen. It seems that age thus forms a threshold in the execution of these various forms of play in the Hartmann zebra. According to Klingel (1967) the young of the Burchell zebra indulge in the same types of game. He also states that the dominant male sometimes joins in these games by playfully chasing the foals. No adult Hartmann zebra, however, male or female, was ever seen to indulge in play behaviour with foals. In further contrast to the Burchell zebra no play between foals of various breeding units was ever seen. This is probably due to the fact that the social units of the Hartmann zebra are much more solitary than the same units in the Burchell zebra. They only congregate in large herds under abnormal conditions, for example when fleeing from a low-flying aircraft. Even when they congregate on green grass after the first rains they are usually, probably owing to the topography of their habitat still widely distributed.

On one occasion a grazing foal came across a flock of guineafowl. He cautiously approached them but they kept on moving away. He then followed them for some distance. This behaviour was no doubt triggered by inquisitiveness rather a desire to play. Apart from this occurrence no behaviour as described by Klingel (1967) of Burchell zebra foals playfully chasing birds and other game was observed in the Hartmann zebra.

Many workers, such as Lorenz (1963); Tinbergen (1951, 1953); Scott (1958); Barnett and Evans (1965) and Ewer (1968), have discussed the functions of play. Most of them agree that one of the important functions of play is that it has survival value for the species. It enhances early general learning which makes the solving of specific problems in later life easier. It also plays a part in the social development of the young, for early social experience is important for normal adult behaviour.

3.3.10.2 Learning.

It is difficult to differentiate between play and learning, because as already showed one of the main functions of play is learning. Not everything, however, is learned by play. Most workers apparently find it difficult to establish which behaviour patterns are innate and which are learned. It is felt however, that some of the behaviour patterns, even innate, still have to be triggered by watching a display of adult animals or through personal experience. From observations in the field this seems to be the case with the Hartmann zebra.

To illustrate the abovementioned, the following examples may be quoted from field notes:

(i) Hierarchy:- In the breeding unit the foals daily experience this behaviour although at this stage it has no marked influence on their lives. Once the female foals become sexually mature, however, they are quickly inaugurated by the older females.

(ii) Ceremonies between dominant males:- On the 29th May, 1970, the two foals of breeding unit 1 were playing. Breeding unit 3 appeared over the crest of a hill some 200 metres away. The two dominant males, 1A and 3A, immediately approached each other and went through their ritualised ceremonies halfway between the two social units. As 1A moved off towards 3A, the two foals stopped playing and followed him. They stood watching the abovementioned behaviour at a distance of 10 metres.

(iii) Mating behaviour:- On the 5th February, 1970, one of the females in breeding unit 5 was in oestrus. On this day copulation was achieved several times by the male. A male foal (three months old) ran around energetically, bucking several times; he then approached another foal (5BA) (10 months old) and mounted him, flapping his penis several times. No doubt this behaviour was induced by the mating activities of the dominant male 5A.

A few minutes later, on the same day, 5BA tried to mount the oestrus female. His mother, 5B, immediately charged the oestrus female (5D) and chased her away.

(iv) Flehmen:- On the 5th February, 1970, a female showed flehmen behaviour. Her three months old foal approached and, apparently copying his mother, also showed flehmen behaviour.

3.4 THE DOMINANT MALE.

3.4.1 Principles of behaviour shown by the dominant male.

In most of the ungulate species some type of natural selection for the males exists. This takes the form of territoriality in some species, viz. the wildebeest, Connochaetes taurinus (Estes, 1968), Grant's gazelle, Gazella granti (Walther, 1965), the Uganda kob, Kobus kob thomasi (Buechner, 1961 and Leuthold, 1966) and the waterbuck Kobus ellipsiprymnus (Kiley-Worthington, 1965). The strongest animals will occupy the best areas in a particular habitat; those animals with the best territory thus have the better chance of rearing their progeny. In this way the most basic concept in the survival of a species is fulfilled - the survival of the genes which is more important than the survival of the individual. In some other species the selection of males takes the form of a harem, where a single male takes possession of a group of females against strong inter-male competition. As one finds with territoriality this latter phenomenon, apart from selection of males also functions as a means of distributing the population to ensure that all available females breed. This is the type of social organization one finds, as has already been mentioned earlier, in the Hartmann zebra.

To ensure the success of this type of social organization the male must possess the following behavioural qualities:

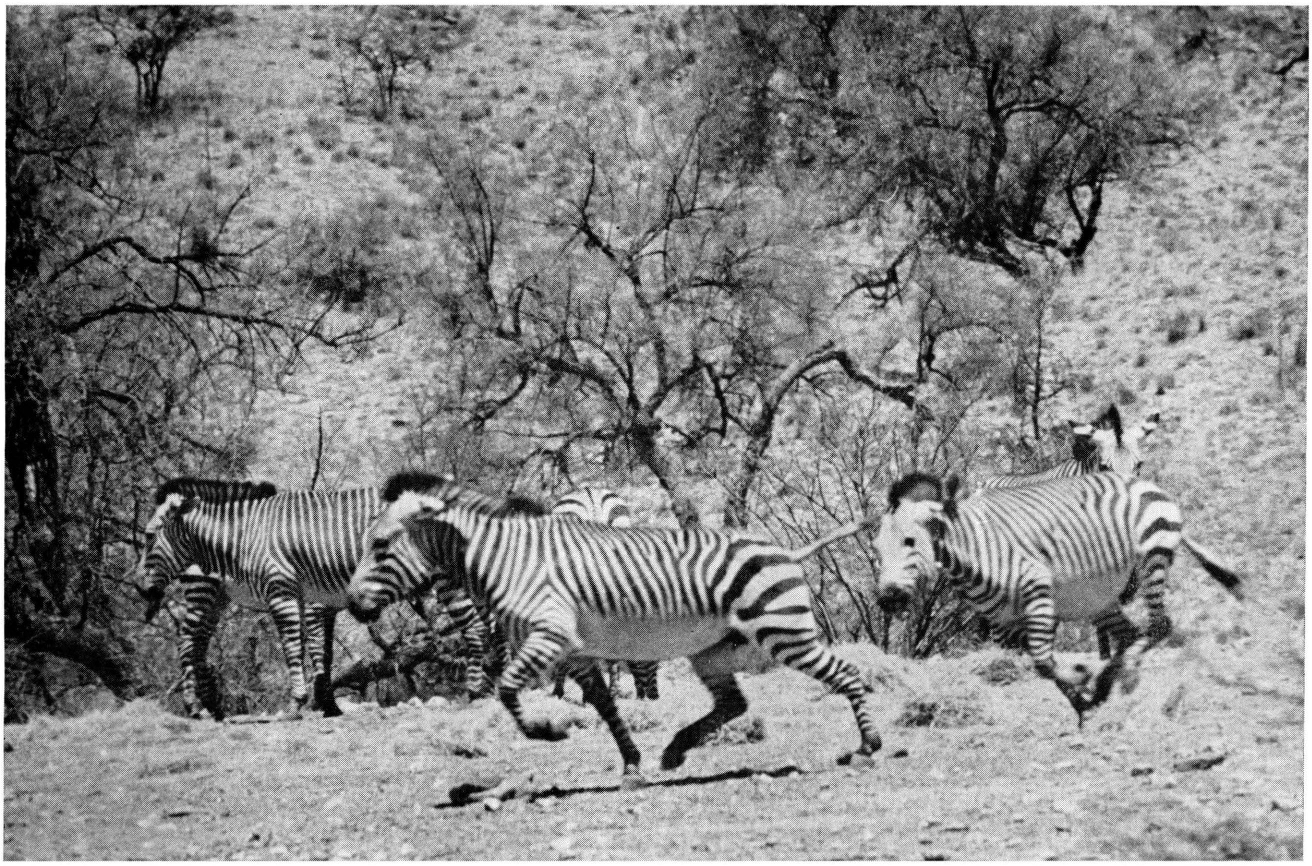


Plate 3: Two females engaged in 'maintenance of hierarchy'' activities. A higher ranking female chasing a lower ranking female.

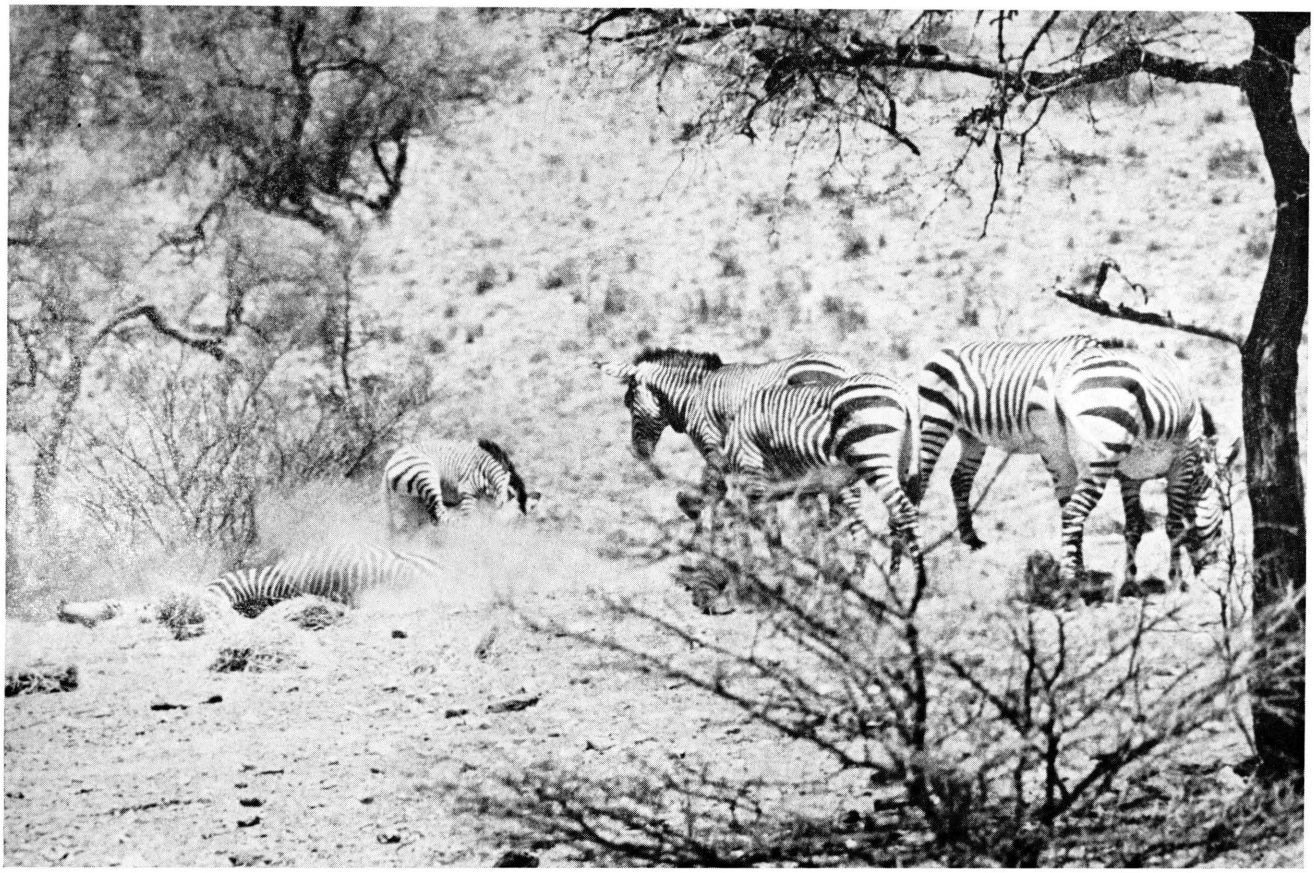


Plate 4: Individuals awaiting their turn at a dust bowl where where dust-bathing takes place in hierarchal order.

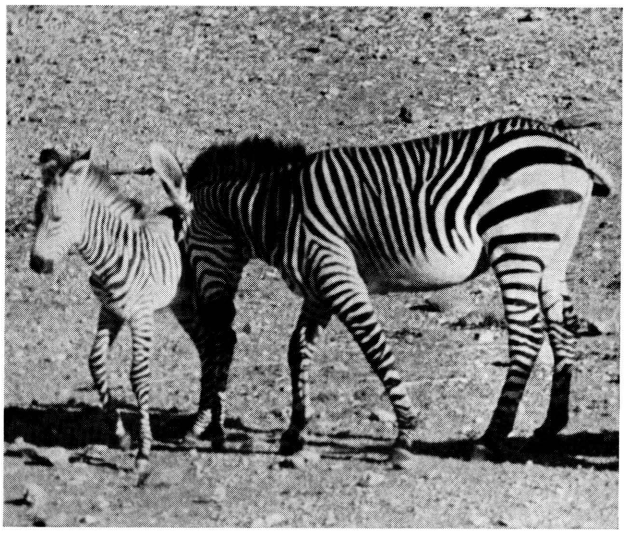


Plate 5: A typical behaviour pattern shown by females towards their foals — female rubbing her face against side of foal.

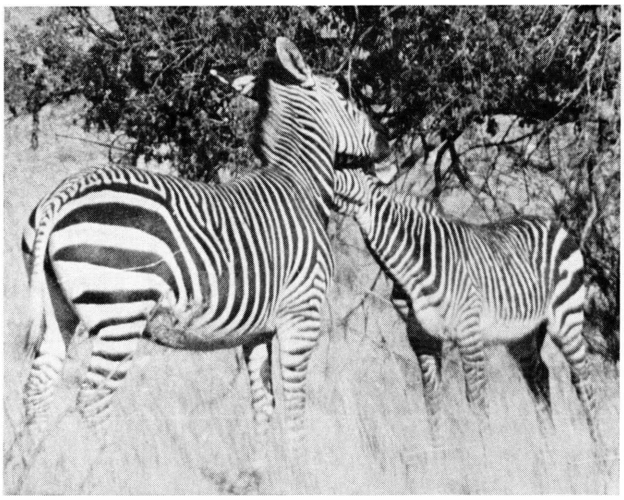


Plate 6: A foal grooming its mother.

Plate 7: A foal laying its neck over that of the mother in an effort to initiate play.

Plate 8: The first step in the challenge ritual between two dominant males, the the *Naso-nasal Contact*.

Plate 9: The *Reverse-Parallel Position* is usually the next step in the challenge ritual.

Plate 10: The *Naso-genital Contact* is also an important part of the challenge ritual.

Plate 11: Two young males engaged in a "greeting game" which is a copy of the challenge rituals of dominant males.

Plate 12: A Hartmann zebra foal suckling.

Plate 13: A breeding unit of Hartmann zebra resting in the shade of trees. Note that the individuals are restricted one to a tree or a female and her foal to a tree. They also show an orientation of their backs towards the sun.

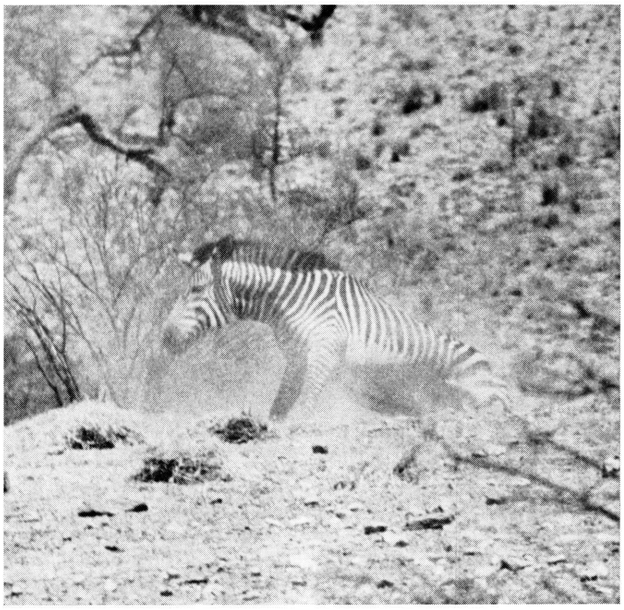


Plate 14: A Hartmann zebra rising with the front part of its body first.

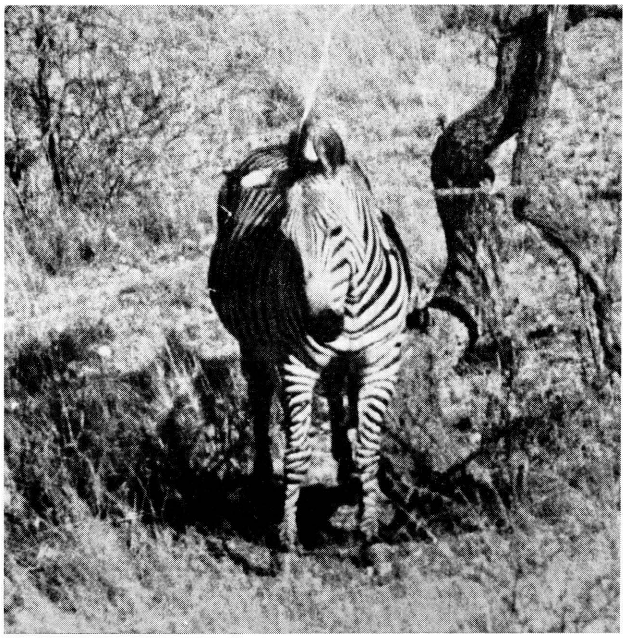


Plate 15: A Hartmann zebra rubbing itself against a tree.

3.4.1.1 Herding behaviour.

The male must possess strong herding tendencies to ensure a female(s) against rivalry from fellow males. That this herding behavioural pattern is very strong is shown by an experience of Mr. Atilla Port, a well-known farmer on the Khomas Hochland. During one of his game capture operations he caught a small male zebra foal not yet six months old. This animal grew up around the house and was allowed to come and go as it pleased. As it reached maturity it was placed in an enclosed camp with a group of springbok and some other game animals.

This Hartmann zebra male was removed from his herd at an age of less than six months and had no contact whatsoever with them afterwards. Despite this it showed herding behaviour and "took over" the small group of springbok. He herded them together and would never let any of the other animals approach close to them. Some time later Mr. Port added eight more springbok to the enclosure. The two springbok groups then tried to join up, but the zebra would not allow it. He intensified his herding activities with his own group and chased the other whenever they approached the first group. At this stage Mr. Port obtained another adult Hartmann zebra male and released it in the same enclosure. This second male showed immediate interest in male one, but male number one only answered with open hostility. The second male was not allowed anywhere near his small group of springbok. Male number two then, after several days, took to herding the second springbok group of eight animals. This led to the two zebra males each having its own 'family' or 'group' which it herded.

If the information above is analysed it shows the following: Male number one was removed from contact with the social organization of Hartmann zebra at a relatively early stage. He did not have the full benefit of learning whilst still with his original family group -

neither did he have any training period with a group of bachelors. Despite this, when he reached sexual maturity he showed herding instincts. It appears as though the need for herding in this zebra male became so great that it was channelled into an outlet by herding springbok. This behaviour was also showed by adult male number two, which had had experience under natural conditions (he was caught while being with a breeding unit), and which also resorted to herding springbok. According to Lorenz (1963) a typical innate behaviour pattern shows characteristic accumulation properties with an increasing need to be performed the longer they are denied an outlet. This indicates:

(i) that in the Hartmann zebra males, herding behaviour has evolved as an innate behaviour pattern.

(ii) that the herding instinct exists and can find an outlet without having to be triggered by an oestrus female although this is normally the case.

3.4.1.2 The ability to face competition and to hold its own against other males.

After a male, against strong competition from rivals, has managed to obtain possession of a certain number of females, it must be able to retain them. Constant rivalry exists between dominant males and this may be considered continuation of natural selection of the males. It ensures that the breeding unit is guarded by an aggressive defender not only against inter-specific enemies but also against intra-specific aggression. In the Hartmann zebra this inter-male rivalry has taken the form of phylogenetic ritualization. Ethologists agree that ritualized behaviour's primary function is that of communication. In this context it fulfils three basic functions in the behaviour of the Hartmann zebra's dominant male:

(i) It suppresses actual lethal contests which endanger the survival of the individual, which is also the carrier of important genes.

(ii) It functions as one of the mechanisms for holding the breeding unit together.

(iii) It is also instrumental in setting up the breeding unit as an independent entity against other similar units.

3.4.2 The influence of the breeding unit on the dominant male.

There is yet another marked resemblance between a social organization based on territoriality and one based on the "harem" system. In most ungulates which show territorial behaviour only the males in possession of a territory will mate. This is found in the Uganda kob (Beuchner and Schloeth, 1965) and Grant's gazelle (Walther, 1965). Estes (1968) is quite emphatic that a wildebeest male without a territory has almost no chance of mating. He furthermore states that both sexual and aggressive behaviour in the male are identifiable with, and only displayed on, a territory.

In the Hartmann zebra ritualized aggressive behaviour and mating behaviour are only shown by a dominant male with a breeding unit. When male 1A managed to take over breeding unit 4, male 4A was forced into a solitary life. He (4A) was challenged on several occasions by dominant males from other breeding units whenever in the same area. This challenge was answered by 4A by either moving away or by submissive behaviour. The same phenomenon was observed in 5A, after being removed from his breeding unit for 27 days for the carrying out of physiological experiments. Within 45 minutes of being released he (5A) was challenged by dominant male 3A. 5A answered with submissive behaviour and anthropomorphically it seemed as though the "solitary confinement" had broken his spirit. He joined his original breeding unit early the following morning. That very same afternoon on being challenged again by dominant male 3A he immediately answered with the ritualized challenge behaviour.

The chance that a Hartmann zebra male without a "harem" will reproduce is even less than with wildebeest males without a territory. Owing to the fact that wildebeest and most Artiodactyls have a definite breeding season with all the females coming into oestrus nearly simultaneously, males without territories or females, sometimes manage to copulate with a female. In the Hartmann zebra it happens very rarely indeed that two females in a breeding unit come into oestrus simultaneously. Should this happen the dominant male is still able to serve both females and keep adversaries at bay.

Another interesting observation in this regard was made. On several occasions it was observed that young females sometimes join up with bachelor units. This normally happened when a female not yet sexually mature and after being driven from the breeding unit, was forced by a gregarious drive to join up with other groups. As the resistance against "strange" animals is at its lowest in the bachelor units it is only to be expected that she should join one of these units. A young female in the bachelor unit in Daan Viljoen Game Reserve came into oestrus. Although five (two fully grown) males were present in the bachelor unit at this stage not one of them mated with her ! As she came into oestrus, breeding unit 6 and the bachelor unit were very close to one another. Dominant male 6A immediately initiated mating behaviour with her. During the following two days he frequently mated with her while the males from the bachelor unit constantly milled around them. They frequently showed flehmen behaviour but not once did any one of the bachelor males try to mount her. One of these males shortly afterwards started his own breeding unit. During all this time the rest of breeding unit 6 was in the near vicinity without taking any interest whatsoever in the proceedings. This indifference in the adult females however, changed suddenly whenever the young female wandered close. They then immediately showed very marked threat behaviour causing the young female to move (instinctively ?) to the dominant male.

From the abovementioned, backed by other similar observations, the following conclusions may be made.

(i) It appears as though the mere presence of a dominant male can inhibit any sexual behaviour by the bachelor males without any physical activity on his part directed at the bachelor males. On other occasions however, bachelor males did succeed in abducting young, in-oestrus females.

(ii) Observations in the field showed that even on occasions when oestrus females were abducted by bachelor males, mating only took place after this herding activity (abducting) was carried out. Apparently herding activity, after being triggered by an oestrus female, is a prerequisite for mating in young sexually mature bachelor males.

(iii) This behaviour by sexually mature bachelor males is indicative of a condition that has been called by most ethologists "psychological castration". The influence of this "psychological castration" is only overcome by bachelor males when they actively engage in herding behaviour.

(iv) The innate herding drive by the dominant male is in an inverted ratio to the number of females in the breeding unit. When the abovementioned observation was made there were six females in breeding unit 6. Apart from mating with the young female, dominant male 6A made no attempt whatsoever to herd her into his breeding unit. This was also observed in the field. The more females in a breeding unit the less resistance was offered by the dominant male to young bachelors attempting to abduct young in - oestrus females. At this stage the keenest competition to the abducting male came from other males in the bachelor unit.

3.4.3 Behaviour towards other dominant males.

In the relationship between dominant males of the various breeding units we once more find a certain resemblance between territoriality and the "harem" organization of the Hartmann zebra. This is the concept of periphery that was first formulated by Frazer Darling (1939) in his study on Rona. Here breeding colonies of sea birds congregate in small areas despite very obvious mutual antagonism and the fact that large tracts of suitable land lie bare. Darling states that conflicts on the territorial border (periphery) is actually a form of stimulation and much sought after. He concluded that one of the important functions of territory is the provision of periphery. Ardrey (1967) comments that these conflicts on peripheries are basic needs of a psychological order, for security, for stimulation and for identity. Estes (1968) reports that the territorial wildebeest male shows appetitive behaviour for challenge rituals on the borders (peripheries) of his territory.

Although Hartmann zebra do not show territorial behaviour, the herding of females against fierce competition by other males fulfils the same psychological functions as the defending of a territory. Hartmann zebra do not have defined borders; the periphery effect is obtained when two (or more) breeding units come close enough to each other to trigger the challenge rituals. As Estes found with wildebeest, Hartmann zebra also exhibt remarkable appetitive behaviour for these encounters. Distances between breeding units when this behaviour is triggered vary, but the average distance is approximately 150 to 200 metres. In denser congregations, on the first green flush after rains, this triggering distance is much less, no more than approximately 30 metres. In more widely spaced populations it has been observed however, that two dominant males might even approach each other from over more than a kilometre to engage in this behaviour.

That the ritualized challenge behaviour by a dominant male towards other dominant males also functions as a mechanism to enforce his position in his breeding unit has already been discussed. That these peripheral conflicts are fulfilling a psychological need for security, as suggested by Ardrey, thus seems to be confirmed by the Hartmann zebra behaviour. That it furthermore serves to stimulate the dominant males also seems to be true. The gusto with which dominant males engage in these challenge rituals, the long distance over which this behaviour is sometimes triggered, as well as the relatively great variety of displays seem to confirm this. Not even the ritualized mating behaviour has the same impact on the observer as the engagement of two dominant males in the challenge rituals.

The third aspect mentioned by Ardrey that this peripherial behaviour is also for identity, is more difficult to confirm. Ardrey (1967 : 171) discusses this at some length:-

> "The animal seeks to differentiate himself from all others of his kind. As a member of a herd or flock ...., the social animal belongs to a group differentiated from all other groups; and within that group he acquires a territory or a rank of status or a perching or resting place, acknowledged as his alone, which distinguishes him from all other members of the group. He has achieved identity".

The dominant Hartmann zebra male achieves both a "harem" of females acknowledged as his alone by fellow dominant males and bachelor males, as well as a rank of status recognized by the females in his breeding unit. Thus according to Robert Ardrey the dominant male in the Hartmann zebra social system has managed to achieve identity.

The dominance relationship between the various dominant males is difficult to interpret. Although special attention was given to this problem, no indication of a rank hierarchy between dominant males could be determined. Theoretically, dominant males should have the same status. In practice however, although no rank hierarchy is apparent, a subtle difference between two opposing males would sometimes be noticed. This is only to be expected with the individual variations that are bound to exist. Another contributing effect might be experience. The longer a dominant male has possession over a group of females the more his self-confidence increases and the more self-assured and agonistic he is bound to be in his behaviour.

3.4.4 Challenge rituals.

In the Hartmann zebra social organization challenge rituals only take place between dominant males. The functions of these highly ritualized activity patterns have already been discussed. Klingel (1967) does not describe any challenge rituals in the Burchell zebra. Although he mentions that fighting between males happens infrequently, it apparently does so with much greater regularity than in the Hartmann zebra, where it was observed only once during three years. Fighting behaviour in the Burchell zebra is not ritualized according to Klingel, but owing to their comparatively harmless weapons no serious injuries are inflicted. The only behavioural trait found in dominant Burchell zebra males that may be compared with the challenge rituals in Hartmann zebra is called "Greeting behaviour" by Klingel (1967). Two of the three components in this behaviour, naso-nasal contact and naso-genital contact described by Klingel, is also found in the challenge ritual of the Hartmann zebra, but the "jump" with which this greeting ceremony is terminated is not present in the Hartmann zebra.

Challenge rituals of various animal species have been described by a number of ethologists. The work by Estes (1968) on the wildebeest is, however, one of the most comprehensive. Many of the terms used by Estes to describe the various positions taken up by the participants, are self-explanatory. In the Hartmann zebra, antagonists take up a few similar positions and the applicable terms used by Estes can therefore be used to describe these positions in the Hartmann zebra's behaviour.

The challenge rituals in the wildebeest are, according to Estes, full of agonistic displays with a rich repertoire of displacement activities. A high degree of individual variability exists in the sequence of events. The challenge rituals of Hartmann zebra have a much more limited display and, probably directly due to this, also show less variability in presentation. It can be divided basically into three steps:

(i) the approach;

(ii) the engagement rituals, which also include several other behavioural traits such as marking, displacement activities and redirected activity; and finally

(iii) withdrawal.

3.4.4.1 The approach.

In contrast to the wildebeest where the head is held low to counteract the impression of menace conveyed by the act of approaching, the Hartmann zebra in the approach is a portrait of arrogance and aggressiveness. This difference can be attributed to the fact that when a wildebeest approaches he is trespassing on somebody else's territory and is psychologically already intimidated. The antagonists in the Hartmann zebra are, on the other hand, always meeting on neutral ground.

The opposing males are already trying to gain a psychological advantage over the adversary by a confident approach. Again, in contrast to the wildebeest where the approach is slow, the two dominant males approach each other at a brisk high-stepping trot. To falter or to hesitate would be fatal. The opposing male might take it as an indication of failure to take up the challenge. While closing in on one another they execute the Head-up Posture with the neck beautifully arched, the ears cocked foreward, straining every muscle and all attention directed at the adversary. No trained show-horse can do any better in an arena.

3.4.4.2 Engagement rituals.

It is here that most of the individual variations take place. These variations, are the result of the various combinations of activities centred around the challenge rituals. The challenge rituals, without consideration of the other activities are discussed first.

When the two approaching males are approximately five to ten metres apart they stop, facing each other heads up. This could be called the Frontal Presentation. This posture can be maintained for up to three minutes. It appears as if this interval is used to size up the opponent. They then approach each other slowly with heads lowered, necks stretched and ears cocked. This posture is very much the same as that described in the ritualized threat behaviour but with the difference that the ears are not laid back against the head. Sometimes one dominant male will stand still, waiting for the other one to approach. They then sniff at each other's noses, making Naso-nasal Contact. This behaviour is followed by what Estes (1968) called the Reverse - Parallel Positio
This position is described as a simultaneous performance of the intimidation Lateral Display. Estes is probably right when he argues that this Reverse - Parallel Position in wildebeest is more appeasing than threatening - a moving into a "neutral corner", so to speak. In this position their horns are out of sight. In the Hartmann zebra this seems to be a more provocative position, as in Grant's gazelle (Walther, 1965), especially if the associated behaviour is considered. This takes the

form of lifting the inner hind leg and feigning kicks backward, indicating willingness to engage in combat. At this stage the Hartmann zebra has two options: it may either indulge in Naso-genital Contact or the Head/Rump Rubbing. Normally however, the Naso-genital Contact precedes the Head/Rump/Rubbing. Contrary to the wildebeest the dominant males do not show flehmen at this stage (it does occur when a dominant male confronts a bachelor unit). The Naso-genital Contact is of very short duration. The Head/Rump Rubbing is, however, normally of longer duration.

Tension is built up through the various foregoing rituals. This tension build-up is also indicated by the tail movements of the participants. In contrast with tail movements induced by insect disturbance, which is always rhythmic, even when the insect disturbance is high, tail movement owing to psychological tension is very erratic. The tail is also lashed from side to side rather than swept. One should bear in mind that the whole ritualized challenge has evolved to reduce lethal fighting. Estes (1968) speculates on the significance of the Head/Rump Rubbing behaviour, as it does not conform with the concept of the challenge rituals being a purely agonistic encounter. Comparing it with similar behaviour in other species he comes to the conclusion that it may be purely social grooming. This seems to be the case in the Hartmann zebra as well, where it functions to reduce the psychological pressure built up.

From the Reverse-Parallel Position the animals circle to the Parallel Position, both animals now facing the same way, from where they again engage in the Naso-nasal Contact. If one of the breeding units is nearby the male whose breeding unit is the furthest will try and break away, apparently to come to Naso-nasal Contact with the other male's females. The second male then immediately answers with a most antagonistic Lateral Display. Standing stiffly erect, neck arched and the head in a Head-up Posture the male blocks the other one's approach. This Lateral Display automatically displays the full size of the individual to the rival. The Lateral Display is also sometimes seen when one of the males wants to disengage from the challenge rituals and the other does not want to allow it. Dominant males also sometimes execute this behaviour to prevent a bachelor unit from making contact with his breeding unit.

3.4.4.3 Demonstration-threat marking.

A very conspicuous behaviour pattern during the challenge rituals of the Hartmann zebra is the way one of the males will stop to either defaecate or urinate. During the course of the challenge ritual they might do both with an interval in between. The other male will then immediately move over and after some prolonged smelling (not showing flehmen behaviour), defaecate or urinate on the same spot. Demonstration-threat marking has been described by various ethologists. In demonstration marking, conflicting (territorial) animals in some species use urinating and/or defaecating in sequence on the same spot as a form of ritualized threat. The fact that this behaviour is noticeable in the challenge rituals of the Hartmann zebra is an indication that it might be a ritualized demonstration-threat marking here as well.

This brings us to another interesting point. Throughout this study various similarities between the territorial and 'harem' social organizations have been noticed. How this demonstration-threat ritual could have evolved out of a territorial organization is not difficult to see. To find the connection between a roving 'harem' type of organization and the marking behaviour is, however, much more difficult. It would seem as though the 'harem' social organization was conceived out of a territorial social organization. The 'harem' organization being an adaptation, although retaining most of the territorial advantages, allows more freedom of movement, thus enabling the animals to cope with changing environmental situations. The demonstrative-threat marking would be a remnant of their territorial past, and did not develop independent of territoriality but is a modification of it.

Other independent factors also support this theory. The evolutionary ancestor of the Equidae was Eohippus, a small antelope-like creature (Colbert, 1961). This animal inhabited forests, and most of the small antelope species still in habiting forests today viz., red duiker, Cephalophus natalensis, and dik-dik, Madoqua kirki, (Tinley, 1969) are strongly territorial. Some of the African Equidae are still territorial today - the Grevy zebra (Klingel, 1969). Therefore it is quite possible that the Hartmann zebra might have been territorial as well.

3.4.4.4 Displacement activities.

When an individual is in a conflict situation, where strong opposing motives prevent him from doing something, the individual may do something neutral. The neutral activity has no superficial connection with the conflicting motives and shows apparent indifference to them. This behaviour is called displacement activity by ethologists (Lorenz, 1966). In interactions between individuals, especially when aggression forms one of the ~~c~~components, the individual may be confronted with the simultaneous arousal of tendencies to advance or withdraw. Thus a conflict situation arises which the animal relieves by the display of a displacement activity.

This displacement activity can take on any form and Estes names a considerable list of activities which are performed in the challenge rituals of the wildebeest. In the Hartmann zebra these 'irrelevant looking actions' during challenge rituals are not so marked. A possible reason is that confrontation between dominant males of Hartmann zebra is not of such a desperate nature. It is also possible that a fleeing male would be followed by some, at least, of his females due to the low threshold of the 'running away' intention movement. And, in effect, be removing his territory with the accompanying part of his harem, thus losing less than would a territorial animal driven from its territory.

The only clear-cut displacement activities that are performed with regularity during the challenge rituals of the Hartmann zebra are grazing and grooming. Displacement grazing takes place at any time during the challenge rituals. Any one of the two animals may break off the challenge ritual for an interval of displacement grazing. This is especially noticeable when one animal indulges in the agonistic Lateral Display, and the other may answer with displacement grazing, or grooming. In this case, grooming consists of rubbing the forehead on the rump of the animal in Lateral Display . This behaviour differs from the Head/Rump Rubbing behaviour described earlier in that only one animal does the rubbing. In the Head/Rump Rubbing both animals do this simultaneously.

3.4.3.5 Redirected activity.

Redirected activity was first described by Tinbergen (1952). He defined it as an

> "activity released by one object but discharged at another, because the first one, while presenting stimuli specifically eliciting the response, simultaneously emits others which inhibits its discharge."

In Hartmann zebra, redirected activity was only seen in the challenge rituals of the dominant males. One of the males would suddenly disengage from the challenge rituals, herd (chase) his females a bit, and immediately return and face his opponent. This behaviour was at first thought to be brought about by the fear that the second male would abduct one of his females. This, however, is not the reason because the herding activity by the male is of extremely short duration and he seldom succeeds in moving the females away. It also does not look as though he is trying in earnest. Furthermore, while he actively engages the second male in challenge rituals, the second male cannot hope to abduct a female. It would thus seem that first male infact wants to chase the second male but the activity is redirected at his females.

3.4.4.6 Withdrawal.

To a certain extent Hartmann zebra have the same problem as other territorial species engaged in territorial border conflicts, that is, withdrawal without losing face. Estes (1968) found that in wildebeest both the approach and withdrawal normally consisted of animals adopting the Grazing Attitude. One of the reasons given for this is that grazing is one of the few maintenance activities that may be continued indefinitely. This is important, as the invader into a territory must somehow again reach his boundary without losing face. With Hartmann zebra, being on neutral ground, this is not so important. To a very great extent they also use the displacement grazing as an exit out of the challenge rituals. But in the Hartmann zebra they only graze for a few minutes and then move away. Sometimes the other participant will follow and again and again do a Lateral Display. In these cases the first zebra keeps on going through the motions of grazing (but walking too fast for any real grazing to take place) until the second zebra also retires. The second zebra may accompany the first for anywhere up to 100 metres. In other instances the participant has been seen to break the rituals off without any ceremony and simply walk away.

3.4.5 Advertising dominance.

With most territorial animals the advertising of ownership of a territory forms an important part of the day's activity pattern. This advertising may take the form of scent-marking territories or sometimes this advertising is vocal, as with birds. Wynne-Edwards (1962) called the morning and evening peaks of birdsong epideictic displays. Estes (1968) found that vocal displays are also used by wildebeest to some extent to warn off conspecifics. He noticed that this calling (grunts) by territorial wildebeest had no influence on females but did have a definite intimidating effect on the passing males, but none on the territorial neighbours.

No evidence could be found in field observations of vocal displays by dominant males purposefully advertising their position. Advertising as such is accidental through other activities, especially exaggerated ritualized behaviour patterns. The more important behaviour patterns here are the challenge rituals, and especially the Lateral Display. This is also used with intimidating effect on the bachelor units. The challenge rituals also fulfil an advertising function to the females in the breeding unit. Herding of his females by a dominant male may in this context advertise his dominant position to other males.

3.4.6 Relations with bachelor units.

An interesting relationship exists between the dominant male and bachelor units. It was found that a bachelor unit would usually 'attach' itself to one specific breeding unit, sometimes for as long as three weeks. During this period it would follow the breeding unit everywhere, down to water and back to grazing. The bachelor unit, however, despite hovering in the immediate vicinity does not get assimilated into the breeding unit. Apart from moving with the breeding unit they do not show the least interest in the breeding unit as such or the social activities within the breeding unit. The females and foals within the breeding unit also completely ignore the presence of the bachelor unit. During this time, the dominant male of the breeding unit to which the bachelor unit has 'attached' itself would spend considerable time fraternizing with them.

This attachment of a bachelor unit to a breeding unit may be due to an innate gregarious drive. The advantages, however, are quite clear. In the first place it gives better protection to the bachelor males owing to the higher degree of vigilance shown by females with small foals. Secondly, it may also function~~s~~ as a sort of training centre.

The behaviour of bachelor males towards the dominant male is one of submissiveness. They constantly mill around the dominant male, uttering the high-pitched submissive call. This specific sound, although also uttered by other animals in the social organization, is almost exclusively associated with bachelor units. It can sometimes be heard long before the bachelor unit is observed. Apart from this submissive call they also execute submissive behaviour such as lowering the heads, but not as low as in the threat ritual and also without stretching their necks.

It is furthermore noticeable that especially the older animals in the breeding unit have prolonged spells of naso-nasal contact with the dominant male. In the naso-nasal contact the neck is stretched foreward, the mouth is opened - without baring the teeth - and with a chewing motion the two animals sniff at each other's noses. It was observed that the Hartmann zebra have exceptionally long, thick hairs scattered on their lips. It may be that this chewing motion is a form of tactile stimulus caused by the long hairs. The fact that it is especially noticed in situations where an attempt is made to avoid aggression between dominant and submissive animals (as between dominant male - submissive bachelor; female - foal; dominant male - female and dominant male - dominant male, but never between females of a breeding unit) makes one wonder whether it does not have a soothing effect on the participants. Klingel (1967) describes naso-nasal contact amongst individuals of similar classifications in the Burchell zebra social system and also in the Hartmann zebra (1968).

The behaviour of dominant males towards the bachelor unit does not follow hard and fast rules; even the behaviour of the same dominant male towards the bachelors is not consistent. One moment he may threaten them with the <u>Lateral Display</u>, not allowing them close to his breeding unit, and then shortly afterwards. they may be permitted to mingle freely while grazing, without the dominant male paying them the slightest attention.

A dominant male, while fraternizing with a bachelor unit, once mounted one of the bachelor males. This behaviour is difficult to understand or explain. Walther (1965) reports occasional mounting following combat encounters between male Grant's gazelles. In this case it would seem as though combat between males is sexually arousing. The encounters between a dominant male and a bachelor unit of Hartmann zebra are far from being a combat situation, so this explanation is not valid. That this behaviour was an attempt at masturbation or homosexuality is also rejected, because if this were the case, one would expect to see this behaviour more often. It may simply have been a sign or indication of superiority by the dominant male over the bachelor male.

3.4.7 Persistence in a breeding unit.

Klingel (1967) observed 41 family groups of Burchell zebra over a period of two years. During this time five family groups had a change of dominant males. Three of these original males died and the other two lost their family groups owing to old age and joined bachelor groups. Klingel observed a further 11 families over a period of one year. In the latter family groups two dominant males were forced to leave their family groups and join bachelor groups. These figures show that dominant males in the Burchell zebra are remarkably persistent in their family groups. In only 14 per cent of the families under observation was there a change of dominant males. During Klingel's study period only eight per cent of the dominant males were forced by rivals to abandon their family groups.

In the study on the Hartmann zebra only those animals in the Daan Viljoen Game Reserve could be observed continuously over a period of three years. Frequent visits were made to the other study areas but the various family groups could only be observed for short periods. Although no figures are available for the other study areas, the overall impression was that in the Hartmann zebra, the dominant male, as in Burchell zebra, shows a high degree of persistence in a breeding unit. This is also borne out by the known individuals at the Daan Viljoen Game Reserve. Over a period of three years the dominant male only changed twice in different breeding units. In one instance the dominant male was forced to abandon this group owing to old age, and in the other instance, the dominant male injured a leg and was eventually forced to abandon his breeding unit as he could not keep up with them.

3.5 THE BACHELOR UNIT.

In the social organization of the Hartmann's zebra the bachelor unit plays an inconspicuous but important role. It serves as a reservoir where sexually mature males are selected for the important function of replacing dominant males who either become~~s~~ senile or are removed by natural causes such as diseases, accidents or predation. It also serves as a 'training centre' where most of the fixed action patterns associated with the dominant male in the social organization are performed. Furthermore, a fact that is not always appreciated, is that the immature animals which leave their breeding units on their own, form easy targets for predators. Owing to a strong gregarious drive however, they are forced into bachelor units where they retain both safety and security.

In the Hartmann zebra young males either join up with existing bachelor units or form new units. Why they should join up with bachelor units has already been discussed. Why they leave their original breeding units is more difficult to explain. Klingel (1967) gives the following reasons for this behaviour in Burchell zebra:

(i) The mother of the foal has another foal and the relationship between mother and foal is broken.

(ii) There are no other males of the same age in the breeding unit, which they then leave to go and look for playmates of their own age.

(iii) A bachelor unit with young foals of similar age may be in the vicinity of the breeding unit, the young of which then leave to join the bachelor unit.

This may be true to some extent but in the Hartmann zebra it still leaves some questions unanswered. Only a third of the foals in any breeding unit leave the unit when the relationship between them and their mothers is broken. From this stage onwards they usually leave the breeding units of their own accord, sometimes more than two years later. One of the first male foals to be born in the Daan Viljoen Game Reserve when this project was started there in 1968 was 5BA. Approximately three months later another male foal 5DB was born. The two became inseparable. They both left the breeding unit of their own accord when 5BA was two years old. They wandered around on their own for almost a week, sometimes in the vicinity of a bachelor unit, before they joined it. In this instance it was definitely not a case of looking for playmates of their own age - they had each other.

There must be some other drive, probably innate, that compels them to leave their breeding units and join a bachelor unit. It may be that this drive is initiated at the time that the mother-foal relationship is severed, but with individual variations. As the foals grow older this drive becomes stronger, the rate of development being a matter of individual variation. When the foals reach puberty the force comes to a head and they must compete (playfight) then with other males. The only males they can compete with are those of approximately their own age in the bachelor units. This competition becomes keener and at a certain point a young in-oestrus female may come along which triggers the herding drive.

3.5.1 Age composition.

It is very difficult to age animals in the field once they are older than approximately 30 months. The age composition of bachelor units is based on the known population at the Daan Viljoen Game Reserve. This information however, was verified with information obtained from the free-living population of the Khomas Hochland. Hartmann zebra were shot on farms to reduce the population numbers and information was gathered for a population dynamics analysis.

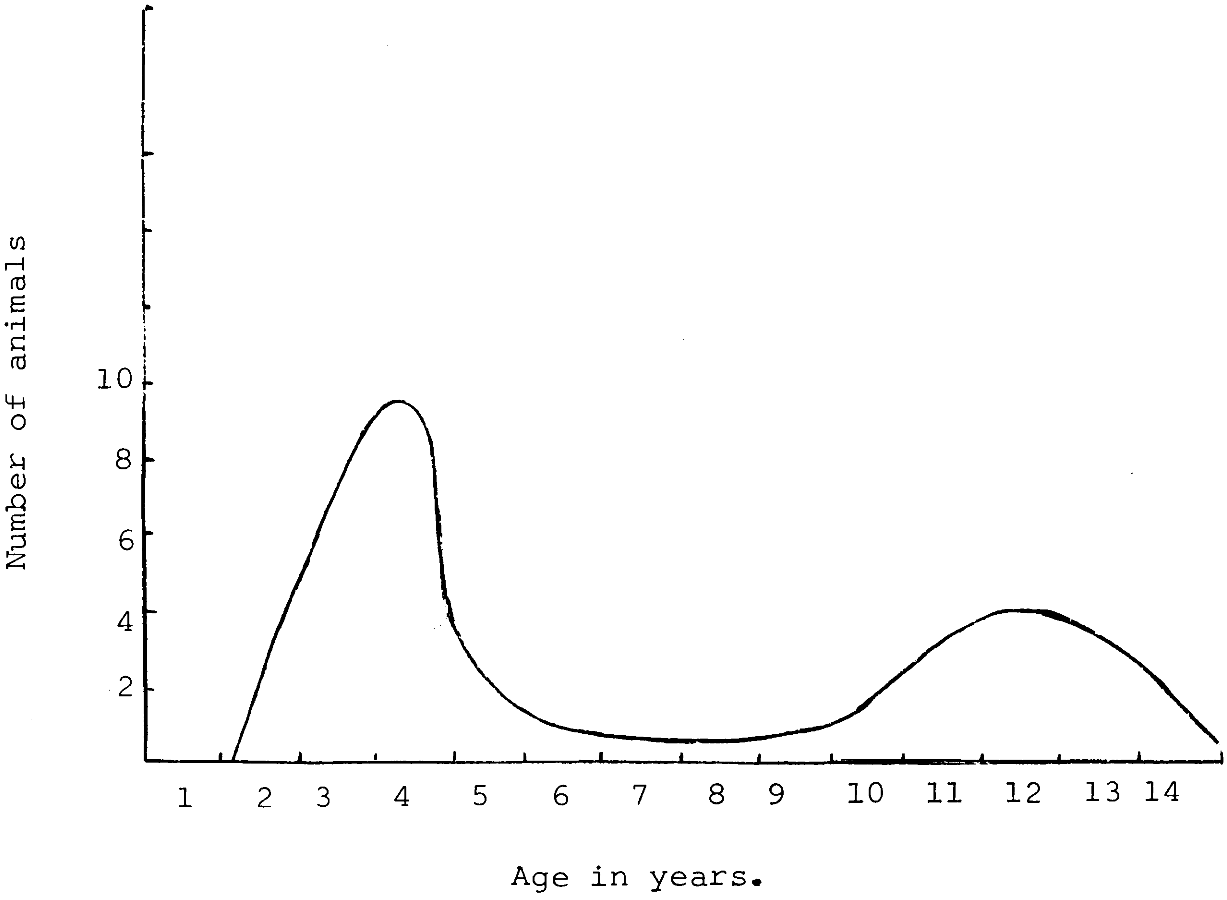
The age composition of a bachelor unit is quite dynamic and shows a constant change as animals come and go. The youngest males might be only 14 months old, whereas the oldest might be quite senile. As can be seen in figure 3.2 a graph showing the age composition of bachelor units shows two peaks. The first peak starts at an age of 14 months and has a steep rise to the apex at approximately four years. From here the graph drops sharply again, virtually to the horizontal axis and stays so low until approximately 10 years. From here the graph shows another gentle rise with a second peak at approximately 12 years. The second peak does not reach the same height as the first peak, however, the reason for this being that the number of the adult males is considerably less, being reduced by predators, accidents, diseases or old age.

It was found that bachelor units consisted of any number of animals between one (invariably adult animals) and 15, the average size being approximately six. The latter, however, may consist of two or more bachelor units that have joined. Usually after a few days they split again into smaller units. It was found that units with only adult animals would on the average be smaller than units that also consisted of younger animals. Although bachelor units frequently existed of only adult animals, one never found bachelor units with only young animals. In the units with predominantly young animals there would always be at least two adult males. In these latter units most of the young animals would have an age of between two and four years.

3.5.2 Internal organization.

As may be expected, the internal social organization of the bachelor units is relatively simple. They spend more time in practising dominant male rituals than in grazing, which occupies more of the breeding unit's time. They spend about 80 per cent of their time loosely attached to sizeable breeding units. Observing them, one gets the impression that the breeding unit innitiates most intentional movements, for instance going down to water. They certainly are very much less vigilant than a breeding unit, and seem to be almost solely dependent on them in this respect.

Figure 3.2: Age composition of bachelor units in *Equus zebra hartmannae*.



3.5.2.1 Relations between bachelor males.

Although the younger males in a bachelor unit are amicable to one another they never become close companions. Although this might be purely anthropomorphic, field observations indicated that the older adult bachelor males do become close companions. Whereas the bachelor units with a preponderance of younger males were usually actively engaged in playfighting or other behavioural patterns, bachelor units consisting of older adult males more often grazed quietly or rested in the shade of trees. They seldom engaged in any playfighting or similar activities.

3.5.2.1.1 Playfighting.

This takes up most of the time of the young bachelor males. Two young males in a bachelor unit will single each other out and start playfighting. Apart from intervals for grazing and fulfilling other necessary life requirements they will continue this playfighting for anything up to two weeks. They bite at each other's knees, bite each other on the mane trying to push each other down to the ground, rear on their hindlegs, pivot around for a better position and knock each other with the shoulders. When one comes across them unexpectedly, it is easy to presume that they are engaged in a battle for life. Only after some observation does one realize that not one of the attacks is really pushed home (although almost so). If nothing else, this form of playfighting is sure to indicate which of the two participants is the strongest and fittest.

During playfighting most of the fixed pattern rituals shown by dominant males in the challenge rituals are also enacted.

3.5.2.1.2 Urination-flehmen sequence.

Klingel (1967) mentions flehmen behaviour shown by young males in the Burchell zebra. They showed flehmen behaviour after smelling at fresh dung or a spot where another member of the bachelor group had urinated. They themselves then in turn defaecated or urinated on this spot. In the Hartmann zebra something almost similar was noticed. The bachelor unit showed this behaviour of defaecation in sequence on the same spot without showing flehmen behaviour. When one of them urinated however, they all showed flehmen behaviour and urinated in sequence. When a dominant male was present this behaviour was even more marked. The flehmen was always followed by extensive naso-nasal contact by all the animals present, intermingled with a clamour of submissive calls, as though the bachelor males were trying their best to ensure the dominant male of their submissiveness.

As already discussed, flehmen behaviour is shown by a great number of ungulate species and is almost exclusively associated with reproduction in most species. Estes (1968), however, observed it also in the challenge ritual in the wildebeest, and has the following explanation for this behaviour in the wildebeest: With the flehmen behaviour the concentration of androgens in the urine offers an index to a male's reproductive - hence territorial - status. He furthermore states that this behaviour during the challenge rituals would be a checking of territorial credentials.

This explanation may also be applicable to the behaviour of the Hartmann zebra, with the various members of the bachelor unit checking each other's reproductive status. The high level of androgens in the urine of the dominant male would thus stimulate submissive behaviour in the bachelor males.

3.5.2.2 Hierarchy.

In the bachelor unit a hierarchy exists but it is not quite the same as the 'pecking order' hierarchy of the females in the breeding unit. The hierarchy of the males is normally not established through serious fighting nor maintained with threat. One may almost call it a 'silent' hierarchy and it is normally related to age and size, with animals of the same age and/or the same size acquiring the same position in the hierarchy.

An amicable atmosphere is present within the bachelor unit.

It is normally the animals highest in the hierarchy which may compete with animals from other bachelor units for oestrus females.

3.5.2.3 New recruits.

New recruits join bachelor units completely voluntary. The younger animals normally join bachelor units which consist mainly of younger animals, and the more adult males join bachelor units consisting of older males.

3.6 FORMING OF NEW BREEDING UNITS.

3.6.1 Influence of oestrus.

The influence of oestrus on the formation of new breeding units is only important under the following conditions:

(i) when the female which comes into oestrus is a young female. Older females which have already become an inseparable part of the breeding unit through their long association with it do not facilitate abducting by young inexperienced males.

(ii) when the number of females in the breeding unit has reached or is close to saturation point. If the breeding unit is still small, the dominant male's own herding instincts will still be so strong that a young inexperienced male would not stand a chance.

(iii) when there is a bachelor unit in the vicinity with sexually mature males which have had the stimulating experience of competition with fellow males and have reached a high position in the hierarchy of the bachelor unit.

Under the conditions mentioned above the oestrus period of a young female serves as a trigger mechanism to ensure keener competition amongst the young males. It is normally at this stage that a certain amount of fighting may take place, usually amongst the higher ranking males of two or more bachelor units. In these cases the males would not have had the chance to meet and test one another in playfighting. The oestrus female also triggers the latent herding behaviour of the young male. The male which finally succeeds in herding (abducting) her, mates with her and forms the nucleus of a new breeding unit.

Field observation at Daan Viljoen Game Reserve has shown that experienced males, that have lost their breeding units owing to some reason or other, do not need the triggering action of an oestrus female to try and form a new breeding unit. Three Hartmann zebra were introduced into a small enclosure behind the Legislative Assembly Buildings in Windhoek. These animals consisted of two males and a female, all unknown to one another, and although the female was not in oestrus, fighting broke out between the males. One of the males, slightly younger than the other, eventually succeeded in ensuring the female for himself. A few years later it was decided to remove the younger male and release him in the Daan Viljoen Game Reserve. Within a week he had a breeding unit consisting of two young females, one having been secured from the bachelor unit. This female had an oestrus period about two months previously. The other young female also did not show oestrus behaviour when she was herded into this new breeding unit a few days later.

3.6.2 Behaviour of female(s) to an encroaching male.

When a dominant male herds a new female into his existing breeding unit, he normally has no trouble in subjecting her to his dominance. It was observed that females in the breeding unit quickly converge on her and settle her into her rightful position in the hierarchy - normally at the bottom. A young inexperienced male or even an older male establishing a new breeding unit, forcibly subjects the new females to his dominance while herding them. During this stage he might actually bite or kick them.

A male that succeeds in taking over an existing breeding unit however, normally faces a dilemma, all the females in the breeding unit face him in a united front of antagonism. Whereas the females normally only threaten one another and their foals in agonistic situations they actually assault the dominant male. This normally consist of kicks aimed at his body but rarely do any harm. The intensity of these attacks diminish in the females with their position in the hierarchy. The lower the rank the less intensive the agonistic behaviour of the female. The social rank of the females also plays a role in their acceptance of the new dominant male, the lower ranking females being the first to accept him and the dominant female normally being the last.

The dominant male accepts this agonistic behaviour of the females stoically. If the attacks gets too intense he retaliates by herding behaviour in which he also may bite some of the females. The whole future of the breeding unit depends on the new dominant male's ability to establish himself in a strong dominant position. With the smaller breeding units this presents no serious problem to the male. In the more sizeable breeding units however, it sometimes happens that the male fails to consolidate himself into a strong dominant position. Should he fail to achieve this the breeding unit disbands, leaving him with only a portion of the original unit. Some of the females and their foals are then taken up by othe existing breeding units. Occasionally the original dominant male regains some of his old unit. This disbanding of the breeding unit is no sudden affair but happens gradually over several months.

3.6.3 'Habituating' of a male.

This is one of the methods by which existing breeding units are some times taken over by a new male. Estes (1968) also describes it as a method which wildebeest males employ in gaining a territory. Maler and Hamilton (1966: 642) discussed habituation and extinction of animal behaviour at some length. They define habituation as the waning of responsiveness to repetitions of a constant stimul~~u~~i, thus leading to the eventual extinction of a conditioned response.

In the Hartmann zebra this method is mainly employed by males which have had experience herding females, normally young males which sometimes quickly lose their first breeding unit. This method is also not directed against vigorous dominant males but only against dominant males which have hurt themselves or are becoming senile. The habituation of a male to a breeding unit was observed several times in the field. At the Daan Viljoen Game Reserve breeding unit 4 was taken over in this way. During February 1970 it was observed that the dominant male's front right leg was quite stiff and swollen at the knee. Over the next few weeks this condition worsened, the joint eventually becoming as large as a football. A few days after the condition of the male was first noticed an adult male (2C) from the bachelor unit joined breeding unit 4. The dominant male immediately challenged 2C, which showed submissive behaviour and retired. He remained in the vicinity of the breeding unit and every time he approached close he elicited aggressive behaviour in the dominant male. This aggression-eliciting distance gradually became shorter and shorter until the male 2C actually joined the breeding unit. Never, however, did 2C challenge the dominant male, who in the end, hindered by his leg, could not keep up with the breeding unit. He was eventually left behind. By this time his general condition had worsened considerably and he eventually died. Males taking over a breeding unit in this way are usually accepted by the females without any trouble.

3.6.4 Splitting of existing breeding units.

As discussed above this is something that happens very infrequently. It only occurs when a sizeable breeding unit is taken over by a new male which fails to establish himself in a dominant position.

3.6.5 Stability of a new breeding unit.

The stability of a new breeding unit depends to a large extent on the new dominant male and his previous experience. It was frequently observed that young males, especially after their first herding activity, may lose their females normally to older, more experienced males who may or may not have their own breeding unit. When a young male loses his female he normally rejoins his old bachelor unit.

3.7 GENERAL DAILY ACTIVITY PATTERN.

3.7.1 Nutritional activities.

3.7.1.1 Grazing pattern.

This behaviour pattern showed daily variations. It is, however, the activity that filled the best part of each day and when compared with other activities, is relatively stable. It was found that not all the animals were grazing at or shortly after first light. Normally, however, from within half an hour after first light the grazing activity intensified to become one of the major feeding periods of the daylight hours. After two to three hours the activity slowed down considerably, with some of the animals grazing while others rested or engaged in other activities.

Even during the rest periods of the day hardly any time passed without some of the animals starting to nibble for a few minutes. The grazing activity intensified again from about 1500 hours and normally reached its highest intensity shortly before last light. During the rest of the day the grazing pattern was rather erratic with feeding activity taking place at a rather leisurely pace.

From the grazing activity graphs (figures 2.1 to 2.12, based on one average day for each month), it will be seen that more than 90 per cent of the individuals in a family group rarely graze together at any one time. This is due to the fact that the activity percentage is based on half-hour time intervals, each consisting of six observations. If, however, the five-minute observation periods are analysed independently, it is found that one hundred per cent of the family groups were observed to be grazing together for 4.8 per cent of the total number of observations per day during February; for October this figure rose to 20.8 per cent. The reason for this increase during October will be discussed under seasonal variations. The periods when 100 per cent of the family group were grazing were normally during the early morning or late afternoons, viz. during the two major daylight grazing periods. The fact that these animals do not normally all graze together at any one time probably results in increased vigilance.

While the animals are grazing there is a slow but almost continuous forward movement. This movement normally takes a zig-zag course. While thus grazing the animal moves a considerable distance to left and right of its forward direction; the zig-zags may be anything up to 100 metres. As soon as the animals come across a patch where the grasses are more palatable, the legs of the zig-zag pattern may shorten to a few metres. This zig-zag mode of grazing nearly always follows the contours of the area in which the animals are grazing. Despite this, the animals sometimes stand grazing with head pointed down the slope or facing up the slope.

Another very conspicous behavioural trait is the lack of synchronized grazing between the dominant male and the rest of the family group. Normally he starts his grazing activities long after the females have started in the morning and may continue some time after they have lessened their grazing intensity. It is doubtful whether this behaviour can be attributed to vigilance on the male's part. During this period of inactivity he always assumes a sleeping posture. Where, on a number of occasions during these periods an alarm was given, it was noticed that it was nearly always done by one of the females. It is of course possible that the male rests after having been vigilant throughout the night. Indications are, however, that the females have to feed longer owing to the drain of lactation.

3.7.1.2 Nutritional activities of foals.

Foals start grazing within a few days after birth, although they remain dependent on their mothers until weaned. Figure 3.3 shows the daylight sucking pattern of Hartmann zebra foals. This shows clearly that although sucking occurs throughout the day, two peak periods exist. These are between 0800 hours and 1000 hours in the morning and then again from 1400 hours onwards in the afternoon, which coincides with the major feeding periods of the breeding unit.

3.7.1.3 Drinking.

Where the Hartmann zebra are hunted they normally come down to water during the night, sometimes before 2200 hours, but more likely during the early morning hours after 0400 hours. In areas where they are protected or not disturbed, as at waterholes high in inaccessible mountains, they drink any time throughout the day. This behaviour was observed at the rainwater pans on the Naukluft Mountain plateau, and certain localities along the Kuiseb River, as well as in the Daan Viljoen Game Reserve. They may visit the water at any time during the daylight hours with peaks from approximately 0700 hours to 0900 hours and again from 1900 hours to approximately 2200 hours. When water is available they may drink daily, sometimes even twice daily, viz., early morning and late afternoon. It is not certain how long they can remain without water during the hot dry conditions but during the rainy season they may go two or more days without drinking (See figure 3.4).

3.7.2 Social activities.

3.7.2.1 Hierarchy.

Activities between the females of a family group to affirm social status occur throughout the day. These activities, however, reach a low point during the two major grazing periods and become more marked again as grazing activities decrease. Figure 3.5 shows a period of high intensity activity from approximately 0900 hours. The other figures (3.9 and 3.11) illustrating comfort movements viz. dust bathing and rubbing, also show increased intensity from about the same time. This increase is no doubt due to the competition for the best shade, rubbing posts and a better position in the dust bathing sequence.

3.7.2.2 Playing.

This activity is indulged in mainly by the foals in a family group and the immature animals in the bachelor groups. In the former, play consists mostly of the running/chasing variety while with the latter it becomes more serious and consists mainly of playfighting. Play occurs almost throughout the day as can be seen in figure 3.6 but with an higher intensity during the morning hours. This high intensity playing from 0700 hours to 1000 hours coincides with the major morning activity period.

3.7.2.3 Mating.

Mating activity occurs throughout the day as shown by figure 3.7. Unlike most other activities, however, it shows a higher intensity during the afternoon from 1300 hours.

3.7.2.4 Greeting rituals.

The rituals observed by dominant males whenever two family groups happen to meet do not vary at different times of the day. This behaviour is caused by the chance meeting of groups and no pattern is discernible.

3.7.3 Comfort activities.

3.7.3.1 Resting.

This is a very marked activity in the Hartmann zebra. A large percentage of the family groups under observation normally sought shelter in the shade. Usually, however, one or two individuals will stay out in the sun, either resting or grazing. Even during some of the relatively cooler winter months they would seek shelter in the shade of trees. As shown in figure 3.8 this happens from as early as 0730 hours in the morning, thus shortly after first light. No animals were ever recorded standing in the shade later than approximately 1730 hours. No clear correlation could be found between the time that most animals seek shelter in the shade and the peak of the temperature curve, apart from a small increase in this activity between 1330 hours and 1500 hours.

When resting, these animals normally adopt the posture shown when in deep sleep. This is by hanging their heads low - below shoulder height - with the ears held at right angles with the rest of the body and parallel to the ground. Depending on the amount of disturbance caused by insects the tail is switched in a regular rhythm.

3.7.3.2 Dust-bathing.

Hartmann zebras are compulsive dust-bathers. This activity is carried out with a very high frequency throughout the day and throughout the year. There is no clear indication of what advantage this is to the animal. It might be to reduce disturbance by insects. However, there is no decline in the rate at which this activity is performed during the winter months when the insects causing the disturbance are virtually absent. from figure 3.9 one may see that dust-bathing shows a clear pattern with peaks after the morning's grazing activity declines and then again before the afternoon's grazing activity reaches its peak. Insect irritation cannot be shown to have any clear peaks. However, there can be no doubt that insects are responsible for a certain amount of dust-bathing especially when the animals are resting in the immediate vicinity of dust bowls. It is possible that this dust-bathing, which also takes place on wet soil, is a 'maintenance of the condition of the hide' activity.

Dust bowls are normally located at predictable places, usually on saddlebacks or ridges of mountains or in the bottom of the valleys that dissect the Khomas Hochland. They are usually situated in sandy or loamy soil and are approximately 2 to 2½ metres across and anything up to 30 centimetres deep. Sometimes there are a few located close to one another. Newly graded roads are also used. To lie down, a zebra bends its forelimbs and stands on its knees. It then lowers the hindquarters to the ground. Getting up it gets onto its knees and then with a jerk pulls the hindquarters onto its feet. While lying down in the dust bowl it lies flat on its side, also resting the head on the ground. It then twitches the tail working dust in between the higher parts of the hindlegs. It will then roll onto its back and back to the orginal position - it never rolls completely over. Foals however, sometimes do. After doing this three or four times it will get up and then lie down on its other side. The whole performance is then repeated. Sometimes the animals will lie in this position in the dust bowl for several minutes before getting up.

3.7.3.3 Lying down.

Adults were seldom seen to lie down except when taking a dust-bath. On the only two occasions that adult animals were observed to lie down the animals concerned were pregnant mares, heavy in foal. In both instances they did not lie down for longer than 25 minutes. Foals, however, lie down very often especially between 0900 hours and 1800 hours with peaks during 0900 hours to 1200 hours and 1600 hours to 1700 hours as illustrated by figure 3.10. The length of time spent lying down varies between 5 minutes and 35 minutes the average being 18.2 minutes (102 observations).

An interesting aspect is that in all the abovementioned cases of lying down the foals did so in direct sunlight. On no occasion was one of them observed to seek the shelter of a tree to lie down in the shade. When lying down they did so flat on their sides with their heads also resting on the ground.

3.7.3.4 Rubbing.

This nearly always takes place while the animals are resting in the shade of a tree or under overhanging rocks. Animals were very seldom seen to interrupt their grazing, just to rub themselves. The boles of trees were used to a very great extent in this activity although rocks were also utilized. The brunt of this rubbing activity was normally directed at the neck and the side of the body. If the bole grew at an angle or if a rock was used, the animal would try and straddle it to rub the insides of the hind legs and the rear part of the body. The face itself was very seldom attended to in comparison with the rest of the body. Only when a broken off branch was available would this be used for scratching around the eyes and ears and sometimes the neck. They often use their hind feet to scratch their faces,(See figure 3.11).

3.7.3.5 Grooming.

No grooming between adults of a breeding unit was ever noticed and only very seldom between mare and foal. Between foal and mare it occurs more regularly. This amicable behaviour by the foal no doubt serves to promote the maternal instinct in the female and also as a mechanism inhibiting aggressive behaviour in the female. When observed between mare and foal as well as between foal and mare it normally consisted of nibbling the neck and mane. No 'licking' was ever seen such as is common with artiodactyls and certain carnivora. (See figure 3.12).

3.7.4 Sanitary activities.

3.7.4.1 Defaecation.

In the field, animals defaecated between three and eight times a day. Figure 3.13 shows clearly that although defaecation can take place at any time during the day, this activity reaches a peak during the morning high intensity grazing period. It was noticed sometimes that when one animal in a zebra group defaecated it acted as an expression movement and nearly all the other animals would then follow suit.

3.7.4.2 Urination.

Urination does not take place simultaneously with defaecation although it can precede or follow it with only a short interval in between. According to figure 3.14 an animal urinates throughout the day, normally between five to thirteen times a day during daylight hours.

3.7.5 Other activities.

Under this heading all the movements occurring in the daily life of the animals, additional to those dealt with above, will be discussed.

3.7.5.1 Walking.

The major activity here consists of walking while not actively grazing. This takes place throughout the day. From figure 3.15 it may be seen that this activity starts in the morning with a high incidence. It then declines gradually; and it suddenly intensifies again to a high peak during the period 1500 to 1600 hours. Most of the other activities discussed elsewhere have a very low intensity during this time interval with the exception of grazing activity which shows a tendency to increase.

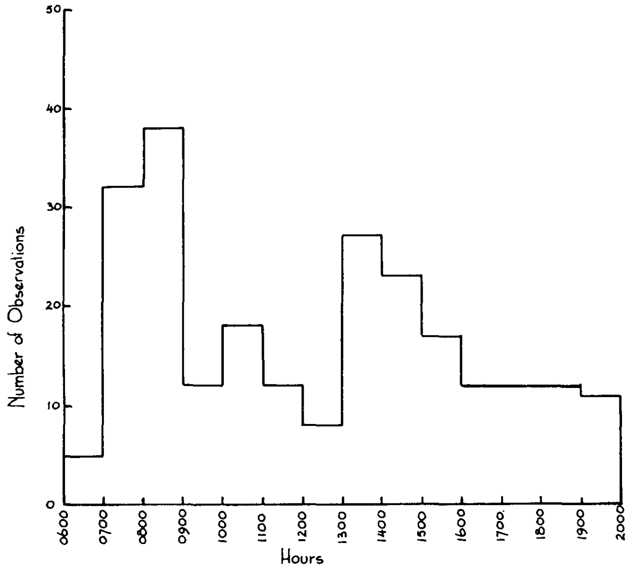


Figure 3.3: Daylight Suckling Pattern of Hartmann Zebra Foals

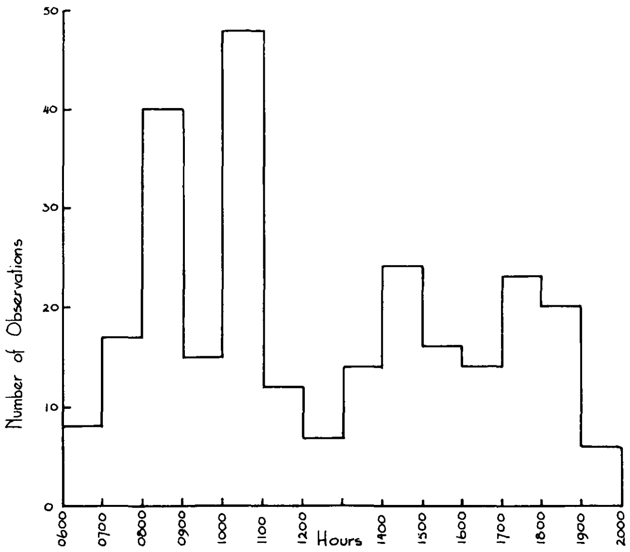


Figure 3.5: Hierarchal activities of Hartmann Zebra Females

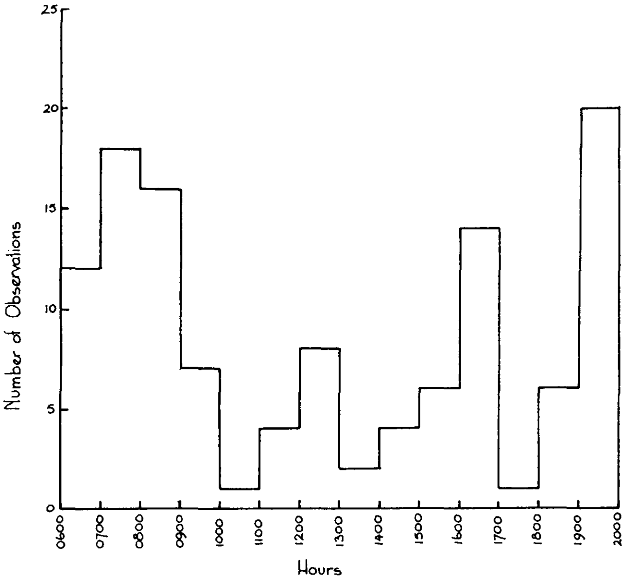


Figure 3.4: Daylight Drinking Pattern of Hartmann Zebra

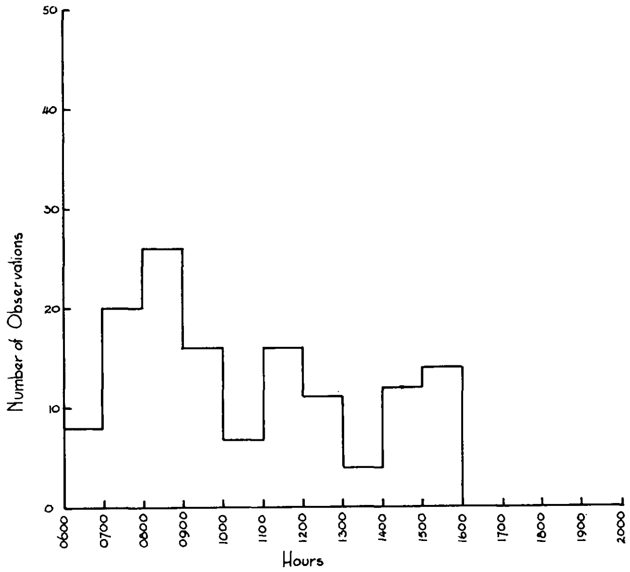


Figure 3.6: Playing Pattern of Hartmann Zebra Foals

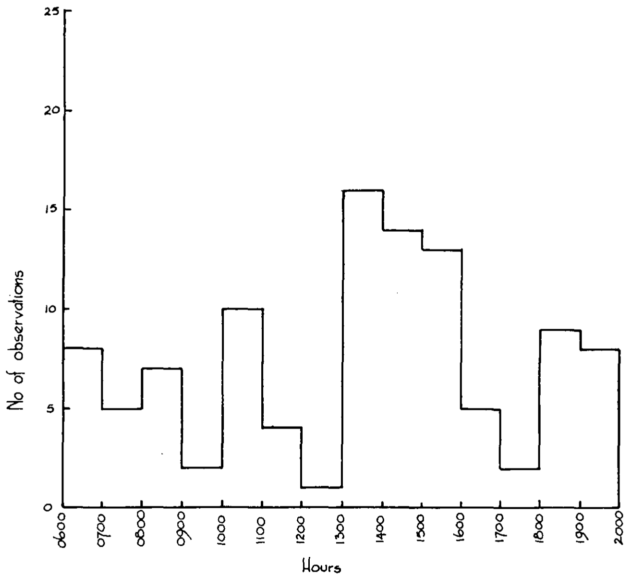


Figure 3.7: Pattern of Mating Behaviour in the Hartmann Zebra

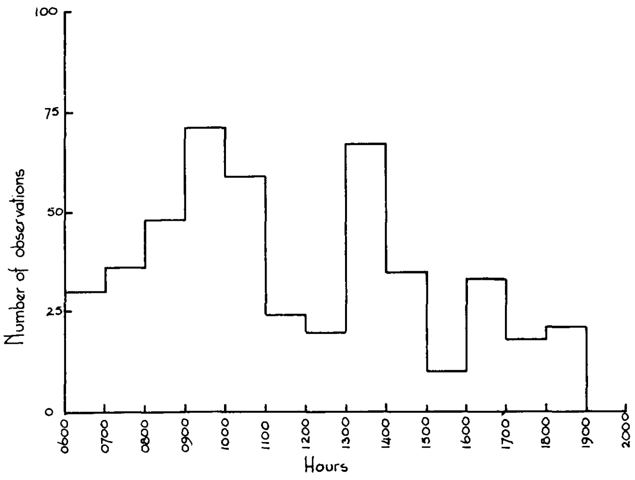


Figure 3.9: Dustbathing Pattern of Hartmann Zebra

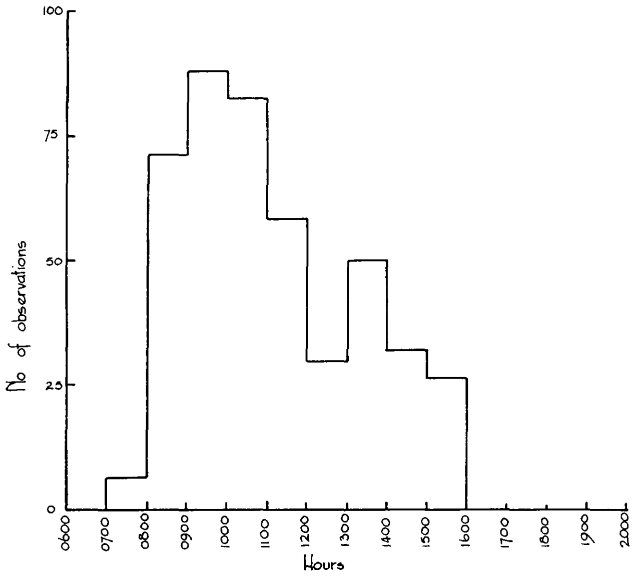


Figure 3.8: Resting in the Shade Pattern of Hartmann Zebra

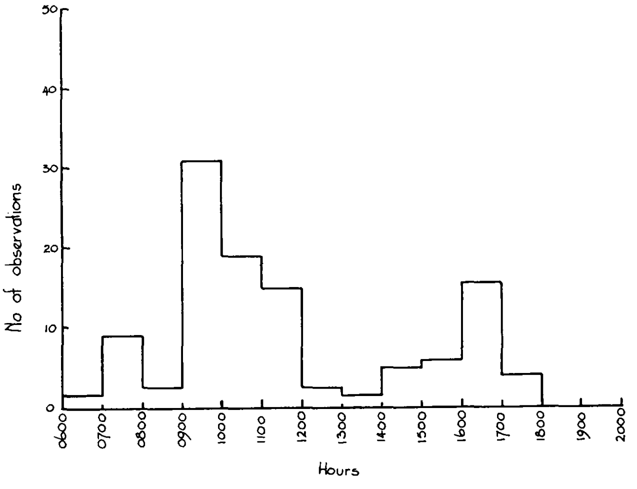


Figure 3.10: Lying down Pattern of Hartmann Zebra

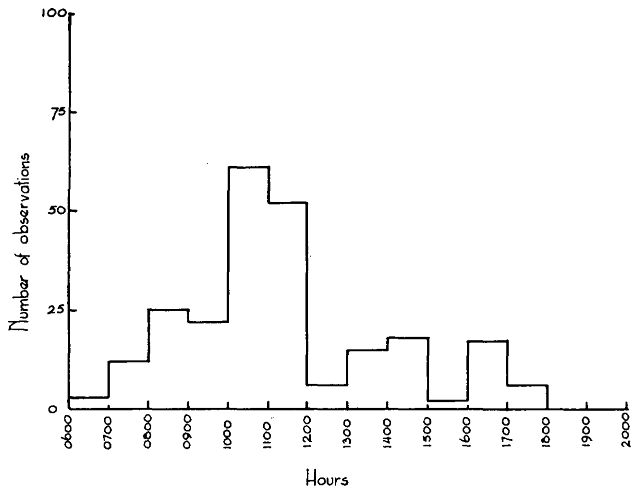


Figure 3.11: Rubbing Pattern of Hartmann Zebra

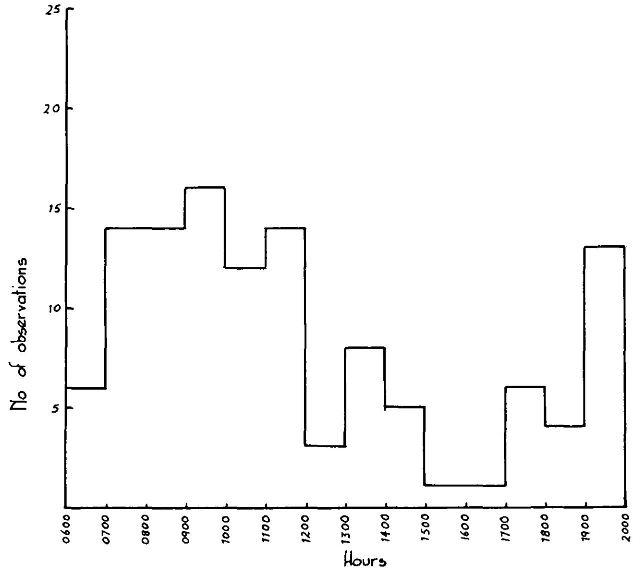


Figure 3.12: Grooming Pattern of Hartmann Zebra

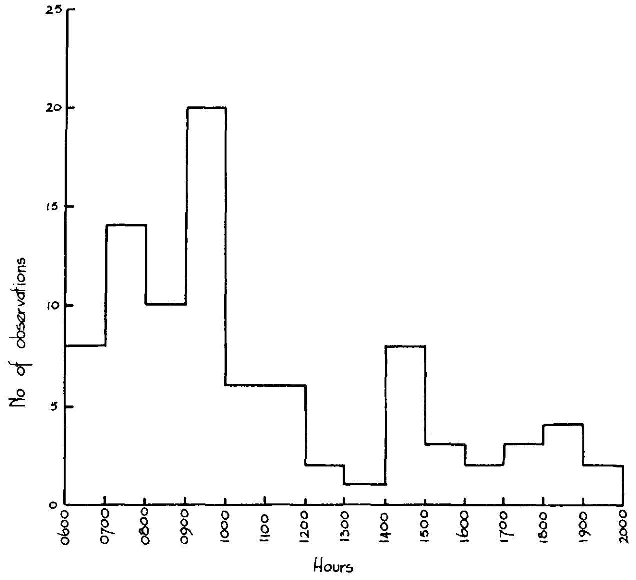


Figure 3.13: Defaecation Pattern of Hartmann Zebra

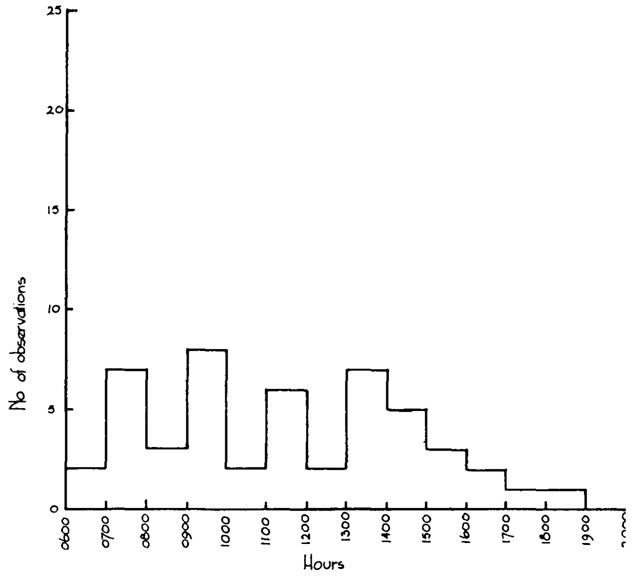


Figure 3.14: Urination Pattern of Hartmann Zebra

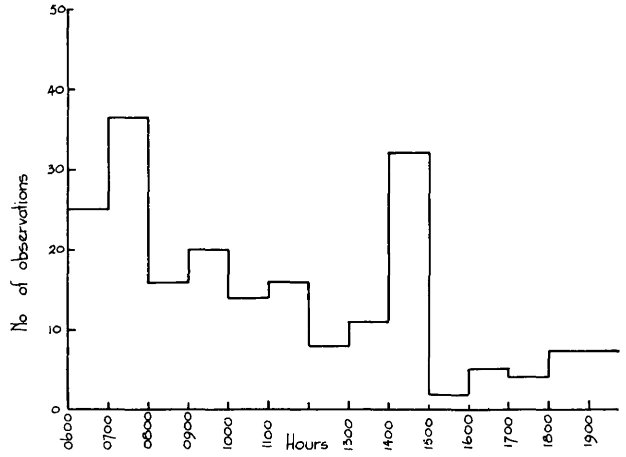


Figure 3.15: Walking without Grazing Pattern of Hartman Zebra

Klingel (1967) found that Burchell zebra have a specific sleeping place to which they retire every evening. In the morning they leave this sleeping place and walk to the grazing area, sometimes as far as 13 kilometres away. No such behaviour was ever noticed in the Hartmann zebra. They would spend their nights anywhere in the Game Reserve and start feeding at that particular place in the morning. The daily distance covered by the Hartmann zebra varies considerably and depends on such factors as condition of the grazing and season of the year. On the average they cover approximately one to three kilometres per day while grazing and, at the most, five kilometres going to water. Even at the Naukluft Mountain Zebra Park and in the Khomas Hochland they are remarkably sedentary.

3.7.5.2 Running.

Running caused by fright or other alarms happens throughout the day with no clear patterns as would be expected.

3.8 HOME RANGE.

With the Hartmann zebra one is tempted to refer to a summer and a winter home range. According to Dice (1952 : 231) however, the home range includes all the feeding sites, breeding sites, places of refuge habitually used by the individual and all the other areas regularly traversed by him. This seems to be the generally accepted idea of what a home range implies and the home range of the Hartmann zebra should therefore include both their summer and winter grazing areas.

This annual movement (migration) of the Hartmann zebra is especially noticeable in the Otjovasandu and Kaokoveld areas where their movements are not yet restricted. They move down onto the pre-Namib flats when the first summer rains fall in this area. They stay here till the onset of the first cold weather when they move back into the protection offered by the mountainous transition belt forming the escarpment here. Even where their movements are restricted Hartmann zebra show this tendency to differentiate in summer and winter grazing areas. The northern part of the Naukluft mountains consist of a gentle undulating plateau. With several depressions which form large seasonal pans during the rainy season. During the rainy season and for the few months afterwards while these pans contain water the Hartmann zebra population of the Naukluft mountains concentrate in this area. As the water dries up they disperse over the rest of the mountain range to perennial waterholes and climatically protected areas.

This seasonal movement is conspicuous even in such a relatively small area as the Daan Viljoen Game Reserve. Although the summer and winter grazing ranges overlap to some extent owing to the restricted area, a definite shift in the preferred grazing area of the population is noticeable. During the colder months they concentrate on the eastern side of the Game Reserve where a high ridge in the west affords protection from the cold western winds. They may be seen early on winter mornings high up on the eastern slopes sunning themselves.

Breeding units have specific home ranges although they may overlap to a considerable extent. Even at Otjovasandu where summer and winter grazing areas were separated by approximately 120 kilometres, recognizable breeding units returned year after year to the same valleys and hills around Otjovasandu. At the Daan Viljoen Game Reserve this was also most marked. With bachelor units, however, the association with a specific home range is much more vague. From field observation it appears that, although they follow the shift in population concentrations, they do not habituate a specific area. They rather attach themselves to a breeding unit for a varying length of time before moving on. One obtains the impression of a continuous movement of bachelor units through the various localized Hartmann zebra populations.

As may be deduced from the abovementioned, breeding units showed marked preference for certain areas within their home ranges. On these summer and winter areas they tended to be very sedentary. Several factors may influence the size of a home range as well as the grazing area, the more important being the area available (thus not restricted by fences or human settlement), the topography of the area, availability of free surface water, vegetation and to a certain extent population pressure. The average size of the winter grazing areas were approximately 6 to 10 square kilometres in the Daan Viljoen Game Reserve compared to approximately 10 to 20 square kilometres at Otjovasandu. On the average the summer grazing areas were considerably smaller than the winter ones.

Although these movements are primarily climatically orientated, as has already been discussed, they ~~have~~ serve a useful purpose. The Hartmann zebra distribution lies for a thousand miles along the Namib desert in a very marginal area. With the low, erratic rainfall, the vegetative cover, especially the grass, is extremely sensitive to overgrazing. Through their migration movements they thus practice rotational grazing, giving certain areas a rest period and a chance to recover. It also serves to ameliorate some of the temperature fluctuations that are so characteristic of this mountainous region along the desert. This differentiation between summer and winter grazing areas shows a remarkable adaptation by the Hartmann zebra to their environment. Even their social system may basically be an adaptation to their environment to establish a relationship of survival for the species as such.

Several very characteristic features are always noticeable on a Hartmann zebra home range, the first of these being the conspicuous dust bowls pockmarking saddlebacks, mountain shoulders and some of the valleys. Just as marked are the trails that connect these various dust bowls only to peter out again; also those trails winding down slopes to waterholes. Some of these go down rather steep slopes although they mostly follow the contours.

3.9 INTERSPECIFIC RELATIONS.

3.9.1 With Burchell zebra.

The only region where these two species overlap is at Otjovasandu and from here northwards through the Kaokoveld to the Kunene River. No marked influence between the two zebra species could be observed. No agonistic behaviour was noted, not even at the waterholes. On one occasion a single Burchell zebra male was seen to graze for a number of days in the vicinity of Hartmann zebra. He did not try to mingle with them but whenever an alarm was given by one of the Hartmann zebra he would also immediately pay attention. Possibly it was for security reasons that he grazed in their vicinity.

No instance of cross-breeding between the two species was recorded.

3.9.2 Other mammals.

Hartmann zebra exhibit no fear towards antelope. Several instances are known where kudu were driven from shade trees by female zebra. The female then utilized the shade herself~~e~~. Even at waterholes kudu and gemsbok moved out of the way when Hartmann zebra came down to water. Once when a zebra female became separated from her breeding unit she joined a herd of female kudu. After joining the kudu she was visibly more relaxed and calm. Hartmann zebra have a definite gregarious drive that force them to join members of their own species. If they do become separated, they join up with members of other species. As has already been stated, this has the combined effect of higher vigilance and security.

Although the threshold for the intention movement of running is very low if other zebra units should start running, other species running nearby seldom cause Hartmann zebra to stampede. Once a herd of approximately 60 gemsbok appeared over a ridge running flat out past a breeding unit under observation. The zebra just watched them galloping past without attempting in the least to join the stampede movement.

In the Ugab valley there are still a number of free-roaming Hartmann zebra, although their movements are becoming more and more restricted by fences. In this area a number of records have been obtained of zebra/donkey progeny observed in breeding units of Hartmann zebra.

3.9.3 Birds.

No red-billed oxpeckers Buphagus erythrorhynchus, occur in the distribution area of the Hartmann zebra but two other bird species, the drongo Dicrurus adsimilis adsimilis and the pale-wing starling Onychognathus nabouroup nabouroup, seem to fulfill the oxpecker's functions in these regions. Actually there seems to be a bit of competition at times as it has been observed that a drongo would chase pale-wing starlings away from a zebra.

Normally drongos perch on a branch close to the grazing zebra unit. As insects are disturbed and fly up, the drongo swoops down to catch the insect in mid-air and then returns to its perch. On a few occasions a drongo was noticed to alight on a Hartmann zebra's back, run back to the tail and while perched there, to pick off the ticks around the anus. Pale-wing starlings were also observed to do the same. A flock would settle at a breeding unit with one or two birds to an animal, and proceed to remove all the ticks systematically.

CHAPTER 4.

POPULATION DYNAMICS.

4.1 METHODS.

The Hartmann zebra in South West Africa are classified Specially Protected Game and under normal conditions no permits are issued to hunt them. During some years, especially drought years when they compete with livestock, permits are issued to farmers. During 1969 and 1970 a number of these permits were issued to farmers all over the Khomas Hochland. Arrangements were made with these farmers and thanks to their friendly co-operation it was possible to collect 128 animals over a period of 12 months.

The animals were shot on a random basis. The method used was modified from the one devised in the Kruger National Park by Pienaar (1969). Numbers, one to five, were written on small pieces of paper with the prefix R or L and then folded. Before a hunt took place lots were drawn to decide which animal of a breeding or bachelor unit would be shot, for example R_2 would mean the second animal from the right or L_1 the first animal on the left.

A list of information and material to be collected from each animal was drawn up after consulting various specialists such as Prof. G. Louw, physiologist, Stellenbosch and Prof. D.M. Joubert, Department of Agricultural Technical Services. A veterinarian or physiologist from the abovementioned Department accompanied the author on several of these hunting trips.

Several practical problems arose. The Khomas Hochland is an extremely broken, mountainous area as already mentioned. The Hartmann zebra has also been ruthlessly (legally and illegally) hunted for the last twenty years and are therefore extremely wild. Hunting these animals turned out to be more easily said than done. Furthermore not all the

Plate 16: A typical Hartmann zebra habitat in the Khomas Hochland. This is where most of the population dynamics work was done.

Plate 17: A Hartmann zebra male being weighed prior to the post mortem.

animals collected could be reached in a vehicle. At first the tripod (three, 3 cms diameter, 4 metres long pipes), scale and all other instruments and sample bottles etc., were carried by hand, in some cases over distances of up to 6 km. During the summer months the pipes forming the tripod became so hot that they could not be handled with bare hands. Eventually post mortems were only done on animals which could be reached in the vehicle or with in easy walking distance of the vehicle. This formed 63.3 per cent (81 animals) of the total number collected.

The standard measurements were taken and the skull collected from every animal in the sample. From those animals on which full post mortems were performed, blood and urine samples were taken, all endocrine glands collected, uteri examined for embryos, smears from the epididymus taken and stained, and samples of the semen taken. All these samples, measurements etc., were given the same number. The skull was also collected and numbered as the rest of the material from that particular animal. All information (date, sex, measurements, weights, pregnant or not, with measurements and weights of ovaries, testicles, embryo/foetus and a list of samples taken) was put on 12,6 cm x 20 cm cards which were given the same number as the animal and then filed.

The skulls were cleaned and sorted into age classes. It was easy to check the weight and measurements of each of these animals later in the various age classes by checking on the number of the skull and then drawing the card with the corresponding number from the files.

4.2 SIZE, GROWTH AND DEVELOPMENT.

4.2.1 Schedules for pre-natal development.

During the study 37 Hartmann zebra mares were collected of which 18 were pregnant. A few more mares may have been fertilized but with the blastocyst so small that it was missed during the post mortem.

TABLE 4.1

SIZE AND CHARACTERISTICS OF THE EQUUS ZEBRA HARTMANNAE FOETUS DURING PREGNANCY.

Gestation period.	Mass (kg).	Length (cms).	Remarks.
1 month		ca 2	The form of the young animal can just be made out.
2 months	ca 0,027	5-7	Although still small certain features viz. the head, body and legs are recognizable.
3 months	ca 0,125	10-15	The reproductive organs are visible. The body is still transparent to a certain extent and the ribs can still be seen. The mouth can be opened and the tongue is fully developed.
4 months	ca 1,0	13-23	Although the body is still naked, hairs can be seen on the upper and lower lips.
5 months	ca 2,7	20-35	The nasal cavities and pinnae are formed.
6 months	ca 3,6	35-60	Hairs on lips, nose, eyebrows and eyelashes.
7 months	ca 4,5	40-70	Hairs on lips, nose, eyelids and tip of tail.
8 months	ca 8,6	50-8'	The mane starts to form.
9 months	ca 13,6	60-90	Hair short and thin on body; darker and lighter bands discernible.
10 months	ca 18,1	70-130	Mane and tail well-developed, complete coverage of hair on body. Hairs short.
11 months	ca 21,6	76-140	Long woolly hair coverage over the body.

Eighteen embryos and foeti in different stages of development were thus collected. This material was then correlated with the characteristics of the equine foetus as determined by Richter & Gotze (1950). By comparing the state of development of the Hartmann zebra foetus with that of the horse and then comparing the weights and lengths, a strong correlation was found. Although the horse foetus and Hartmann zebra foetus showed the same growth in length, the Hartmann zebra foetus did not gain weight as fast as the horse foetus. Despite this, however, the work by Richter & Gotze (1950) was found to be a valuable guide line. The determination of the period of conception of each embryo was based on their work, using both weight and body-length as parameters. The actual description of the foetus however, was made from the specimens to hand.

In figures 4.1 and 4.2 the growth in weight and length of the Hartmann zebra foeti can be seen. According to figure 4.1 the foetus starts picking up weight at an accelerated rate from about eight months. At birth the foetus may weigh 25 kg (n = 5). The increase in body length of the foetus shows a more gentle curve. At birth a foal is on the average 120 cms long (head and body n = 5).

4.2.2 Post-natal development.

4.2.2.1 Weight.

Figure 4.3 shows the increase in weight in the Hartmann zebra. The female weight gain curve levels off sooner than the curve showing the male weight gain. No such marked dimorphism could be determined in the body measurements and skeletal growth.

The average weight of the adult female, older than four years, is 276,3 kg (n = 23). The maximum weight recorded for a female was 322,1 kg. The males only reach their maximum mean weight from (approximately) the age classes XI to XII i.e. from about seven years of age. The average weight of adult males, older than four years, is 298 kg (n = 22). The average weight however, of males older than 7 years is 336 kg (n = 13). The maximum weight recorded for a male was 371,9 kg.

4.2.2.2 Body measurements and skeletal growth.

Body measurements and growth are depicted in figure 4.4. No statistical meaningful differences in the growth rate of males and females could be determined. Even the actual differences in the maximum measurements were slight. As can be seen from figure 4.4 the tail and ear are the first extremities to reach their full length. In contrast to the weight gain the skeletal growth has been almost completed at age class VI - thus at 2½ years. The increase in body measurements from here onwards is slight. As can be seen from figure 4.5 the same is true for the increase in skull length, as well as the length of both the pre-molars and molars combined.

4.3 TOOTH DEVELOPMENT AND AGE DETERMINATION.

The age determination of mammals involves the use of a variety of criteria. The more important parameters normally used are weight and body measurements or the tooth eruption and replacement. The latter has proved to be a most accurate and reliable method in the domestic horse. A rich source of literature in this regard is available, the more important being that of Butz & Böttger's (1946) richly illustrated booklet on tooth replacement in both upper and lower jaws, Duerst (1922), Habermehl (1961) and Henkels (1921).

Apart from publications on the structural differences of the teeth in the various species of Equus (Cooke, 1943; van Hoepen 1932, 1946; Gidley 1901; Haughton 1932), there are two dealing with age determination in zebras by means of the teeth. The first is that of Erz (1964) who evaluated 1,100 skulls of *Equus burchelii* Gray from Rhodesia, but only worked on the order of tooth eruption and replacement. Erz states that the order of tooth eruption and replacement is similar to that of the domestic horse, *Equus caballus*. Klingel & Klingel (1966) published a report on tooth eruption and age determination in the plains zebra *Equus burchelli boehmi* Matschie, and their findings correspond surprisingly well with

Figure 4.1:

Prenatal growth in weight of Equus zebra hartmanna

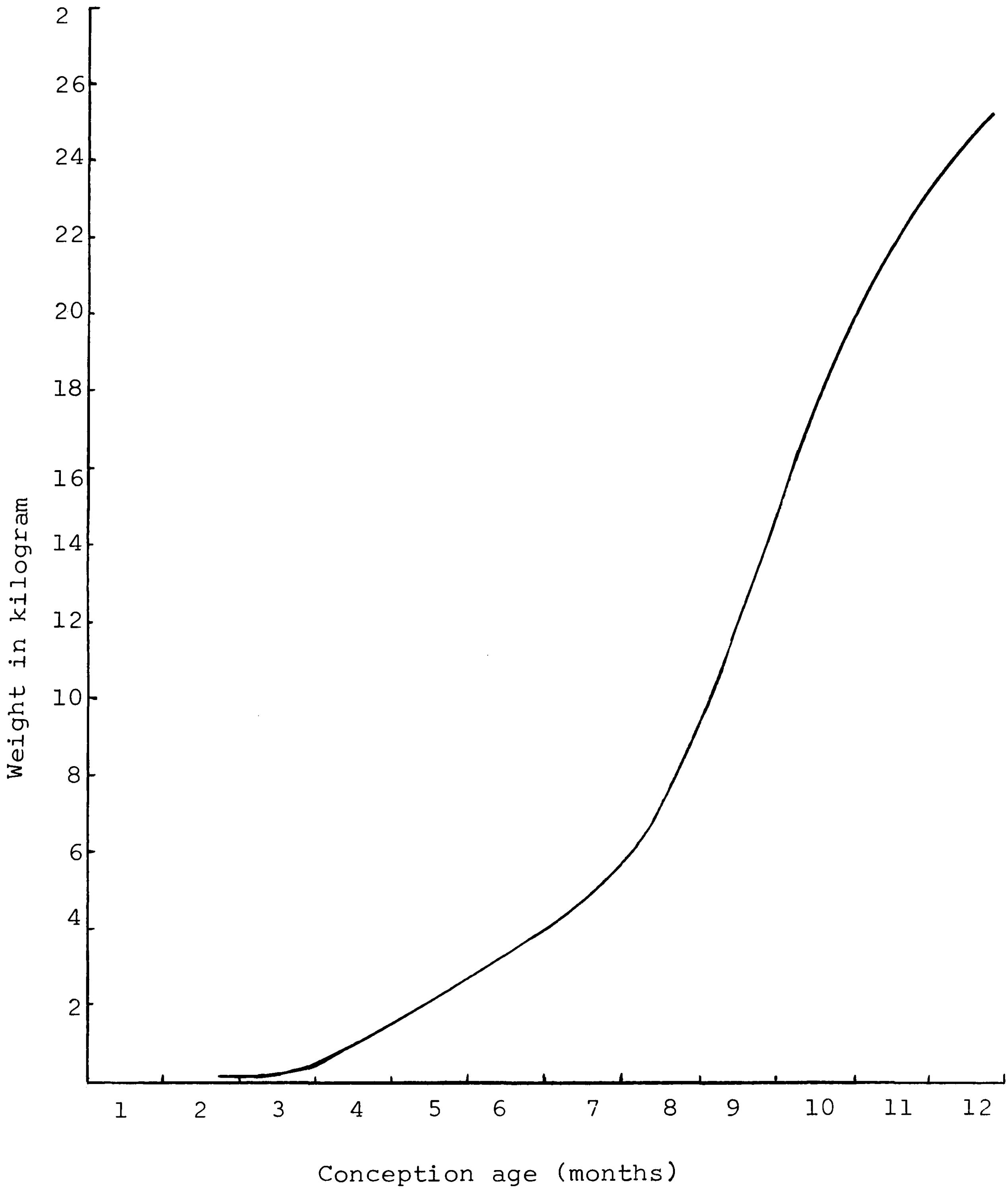


Figure 4.2.

Prenatal growth in length of
<u>Equus zebra hartmannae</u>.

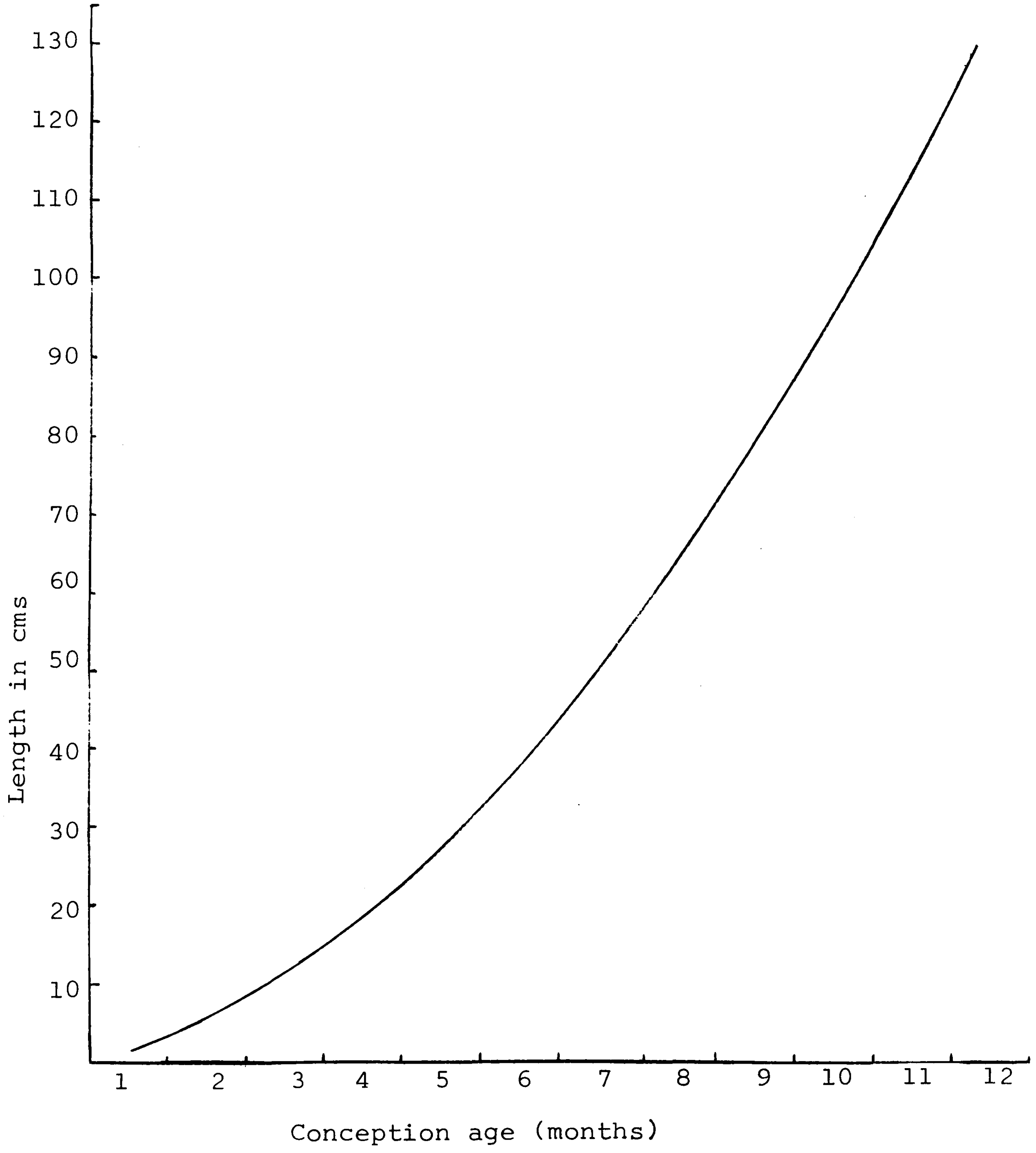
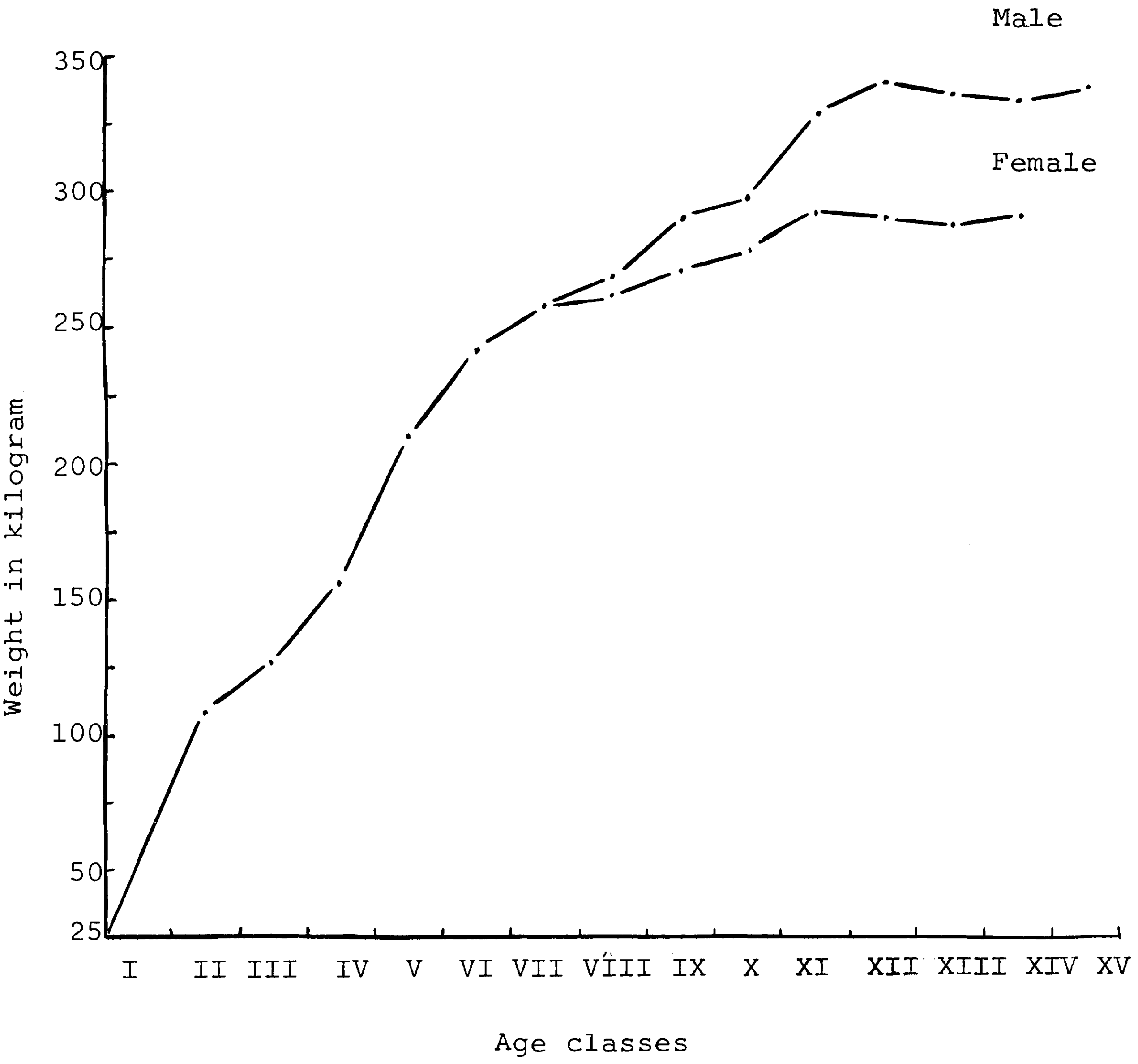


Figure 4.3:

Postnatal weight gain of *Equus zebra hartmannae*.



Duerst's findings in horses. The eruption of I_1 takes place at the same time in both the plains zebra and the domestic horse at 2½ years. This was also established to be the case in the Hartmann zebra.

During the research project on the Hartmann zebra 128 skulls were collected. A study of these skulls showed that the eruption of deciduous and permanent teeth from the bony alveoli in the jaw showed the same pattern as described by both Erz (1964) and Klingel & Klingel (1966). The different stages of wear of the incisors also agree with the findings of Klingel & Klingel (1966), Duerst (1922) and Butz & Böttger (1946) - the latter two publications dealing with horses.

As in the domestic horse and the two zebra sub-species mentioned above a clear dimorphism exists in the milk and permanent incisors. The milk incisors show the prominent neck that is absent in the permanent incisors. The infundibuli of the permanent incisors are much deeper than those in the milk incisors.

The sexual dimorphism in the skulls is shown by the prominent canini in the male. In the female the canini remain rudimentary. The milk canine is visible in the young male as well as female animals from approximately 6 to 9 months of age. It occurred in 41 per cent of the skulls. Rudimentary canines were present in 46 per cent of the females older than two years. Klingel & Klingel (1966) recorded this phenomenon in only 25 per cent of female skulls of the Burchell zebra.

4.3.1 Tooth eruption and order of replacement.

As already mentioned the dentitional formula of all living Equus species is the same. The complete milk dentition in the zebra is:

$$\mathrm{id}\ \frac{3}{3}\ \mathrm{cd}\ \frac{1}{1}\ \mathrm{pd}\ \frac{4}{4}$$

id = deciduous incisors
cd = deciduous canines
pd = premolars.

The permanent dentition is:

$$\mathrm{I}\ \frac{3}{3}\ \mathrm{C}\ \frac{1}{1}\ \mathrm{pd}\ \frac{1}{1}\ \mathrm{P}\ \frac{3}{3}\ \mathrm{M}\ \frac{3}{3}$$

I = incisors
C = canines
pd = first premolar
P = premolar
M = molars.

4.3.1.1 The deciduous dentition.

The discussion on the order of tooth eruption is based on the 128 skulls of Hartmann zebra collected and correlated with the work done by other authors.

(a) At birth the foal has the following milk dentition, first incisor, with the second, third and fourth premolar erupted. Klingel & Klingel (1966) records that in the Burchell zebra no incisors are visible during the first week, but can be felt through the gums. In the several late term foeti of Hartmann zebra examined the incisors were quite visible but covered with a thin transparent membrane. At birth or very shortly afterwards this membrane is absent.

(b) Within a month or two the second pair of deciduous incisors cut through the gum and come into wear. During this stage the first premolar makes its appearance. The first premolar is not replaced by a permanent tooth. Klingel & Klingel (1966) report the first premolar to be present in all the skulls of young animals up to two years of age. In the Hartmann zebra it was present in 90 per cent of the skulls examined, sometimes only in one (upper or lower) jaw. From the age of 2½ years and older the first premolars were found in 27 per cent of the skulls examined, in 10 per cent of these only on the one side (left or right). The first premolars seemed to be replaced by the other permanent premolars in most of the cases.

(c) The third deciduous incisor only cuts through the gum from approximately six months onwards and it normally takes another six months before it is in wear. The deciduous canine normally erupts at the same time.

4.3.1.2 The permanent dentition.

(a) M_1 is the first permanent tooth to develop and erupts almost simultaneously with the third deciduous incisor.

(b) The second permanent tooth to develop is M_2.

(c) From this stage onwards the replacement of the milk dentition by permanent cheek teeth seems to take place almost simultaneously. The permanent second and third premolar replaces the deciduous counterpart and M_3 erupts. I_1 replaces id_1.

(d) I_2 and then I_3 replace the milk incisivi. P_4 comes into wear. During this period the canine also appears.

Figure 4.4:

Growth in post-natal body dimensions of
Equus zebra hartmannae.

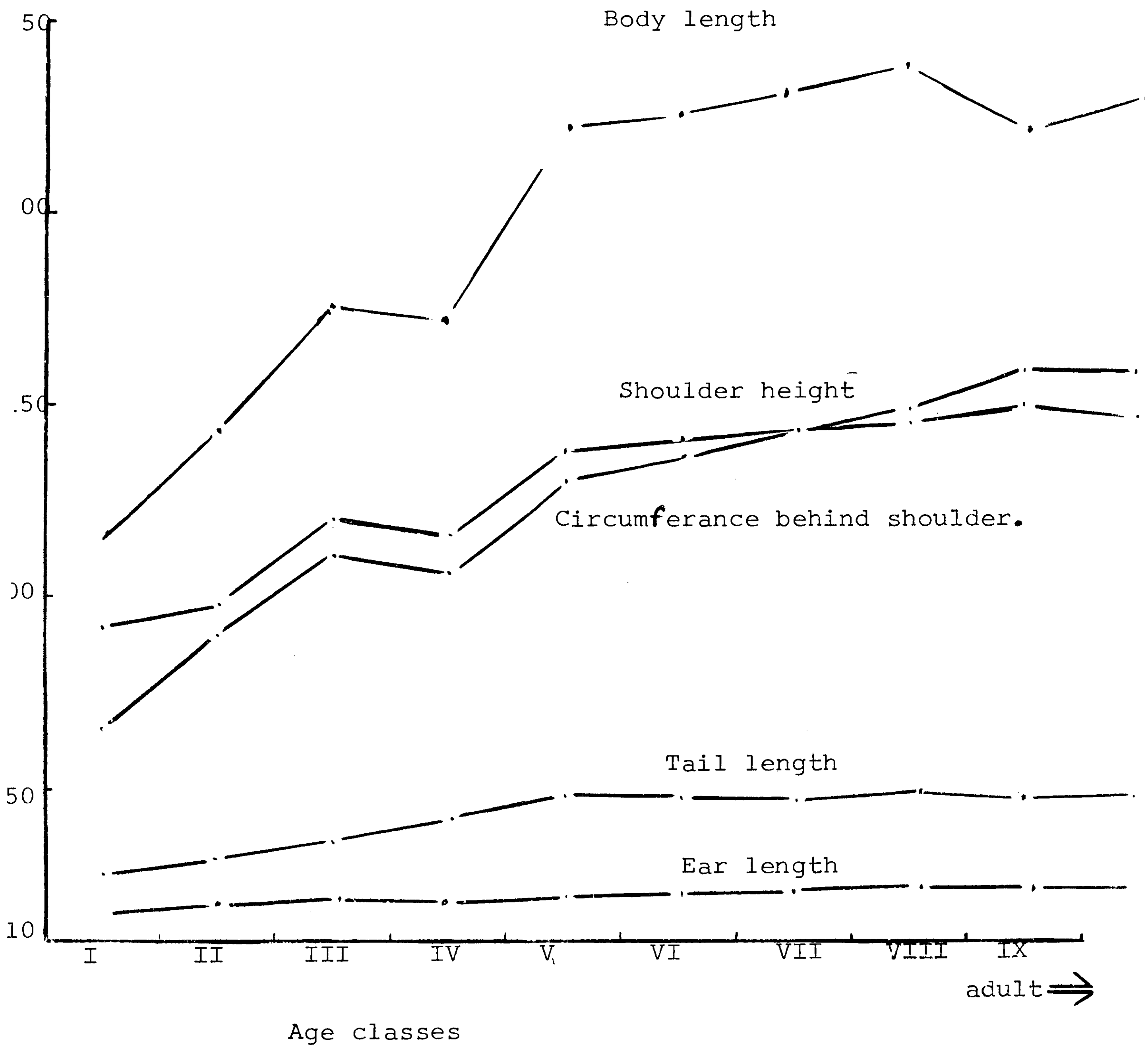
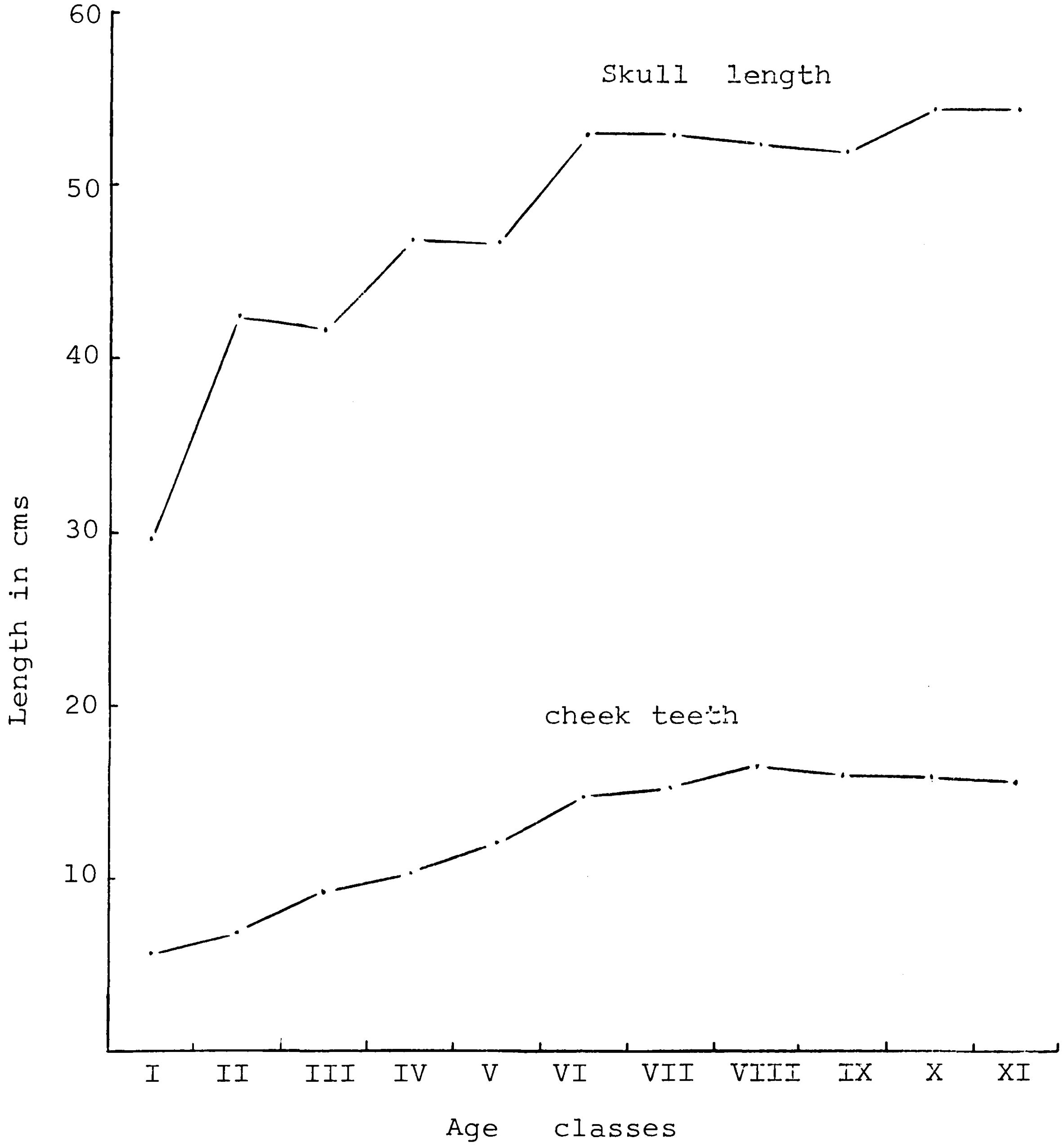


Figure 4.5

Growth of the skull and cheek teeth of *Equus zebra hartmannae*.



Although the samples of Hartmann zebra skulls examined showing the development and replacement of dentition numbered 54, they showed no marked variations. Erz (1964) however, mentions some small variations in the Burchell zebra. At about four years of age Equus has a complete permanent dentition.

4.3.2 Age classes.

Although several publications are available on age determination in the domestic horse, only the publication by Klingel & Klingel (1966) deals with age determination in zebra older than four years of age. This work, however, shows a similarity to the publication 'Das Zahnalter des Pferdes' by Butz & Böttger. Both the abovementioned publications were followed to some extent in working out the following table. Klingel & Klingel (1966) recognize 21 age classes or 'stages', while Butz & Böttger recognize even more (more than 30). It was found, however, that certain of these stages overlapped to such an extent that one had to be too subjective in deciding to which age class a skull belonged. For practical reasons therefore, these age classes or 'stages' were reduced to 15 in this present paper. For details see table 4.2. Only three skulls, approximately two per cent, were found to be in the last two age classes.

TABLE 4.2

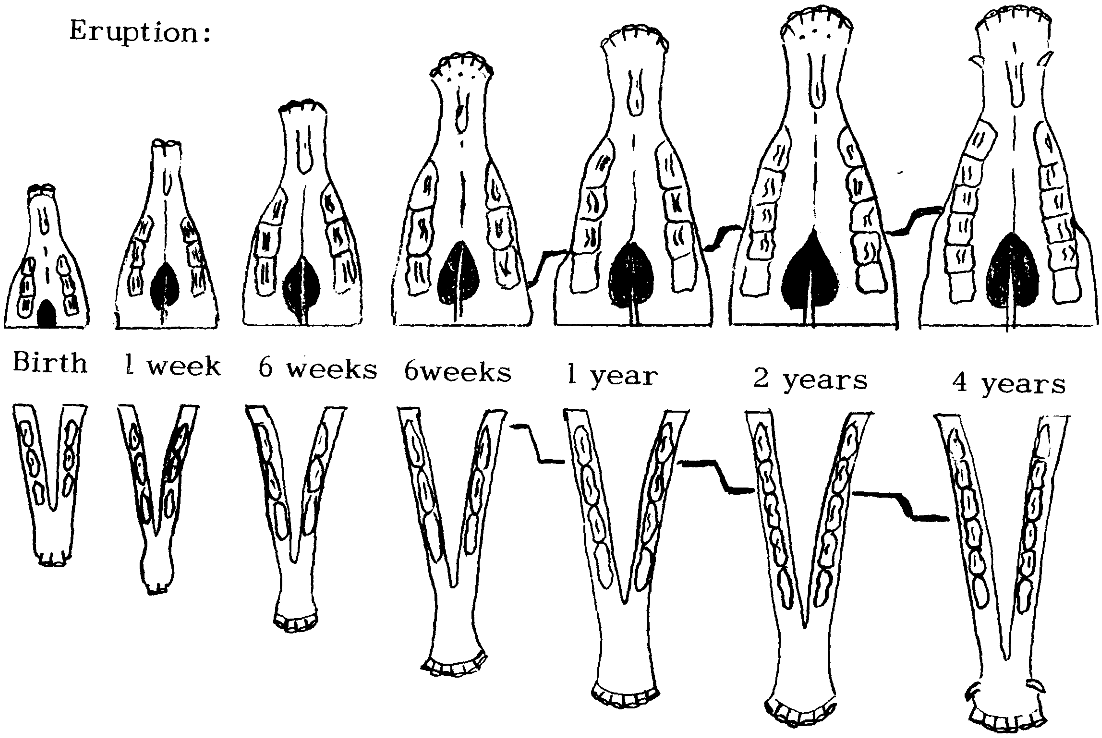
AGE CLASSES BASED ON TOOTH DEVELOPMENT AND
WEAR IN *EQUUS ZEBRA HARTMANNAE*.

Age class.	Age.	Characteristics.
I	Birth to few weeks.	id_1 erupted and in wear. pd_2 to pd_3 in wear.
II	One to three months.	id_2 erupted and in wear.
III	Six to nine months.	id_3 erupted but not yet in wear.
IV	One year.	id_3 in wear. M_1 erupts.
V	Two years.	M_2 erupts and starts to wear.
VI	2½ years.	I_1 replaces id_1, not yet in wear.
VII	3 years.	M_3 erupts. pd_2 and pd_3 replaced by P_2 and P_3.
VIII	3½ years.	M_3 starts to wear. pd_4 replaced by P_4. C erupts. I_2 replaces id_2 and wear.
IX	4 years.	I_3 replaces id_3 not yet in wear. M_3 in wear.
X	5 to 6 years.	I_3 in wear. Infundibula of I_1 oval, of I_2 and I_3 long.
XI	7 to 9 years.	Infundibula of I_1 round-oval, I_2 oval and I_3 long-oval.
XII	9 to 11 years.	Infundibula of I_1 round, I_2 round oval.
XIII	11 to 12 years.	Infundibula of I_1 absent, I_2 round.
XIV	13 to 14 years.	Infundibula of I_3 small and round.
XV	15 years plus	Infundibula of I_3 absent.

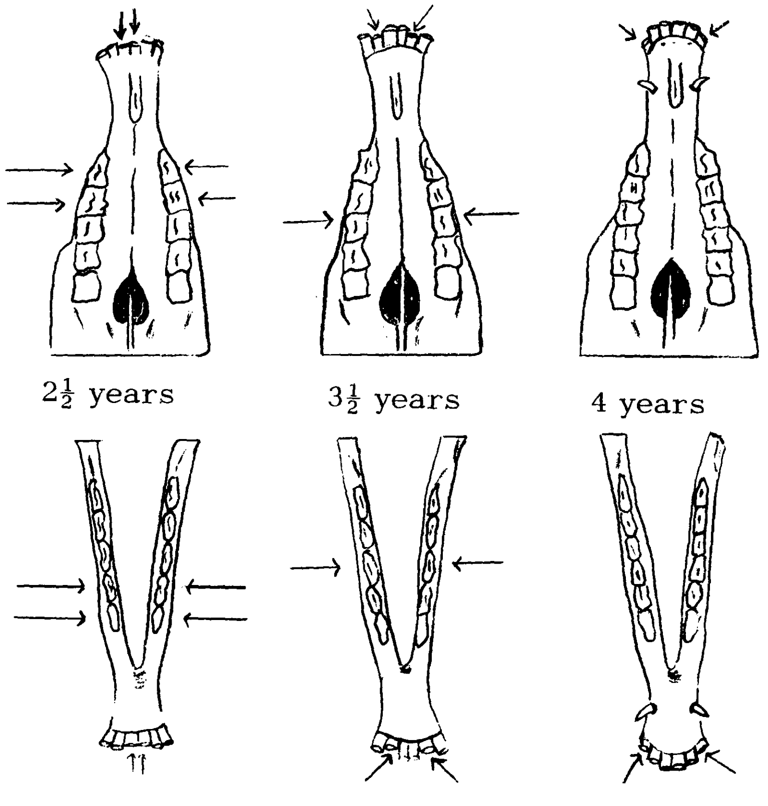
Figure 4.6.

The eruption and displacement of teeth in the *Equus zebra hartmannae* (After Gutz & Böttger).

Eruption:



Displacement:



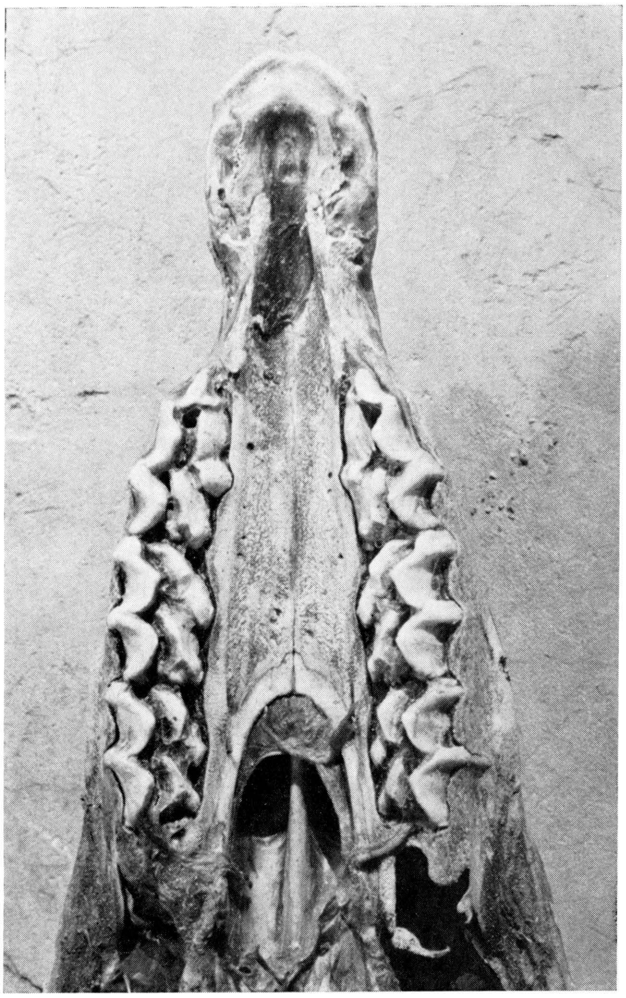


Plate 18: Age class I, birth to a few weeks, pd_2 to pd_4 in wear.

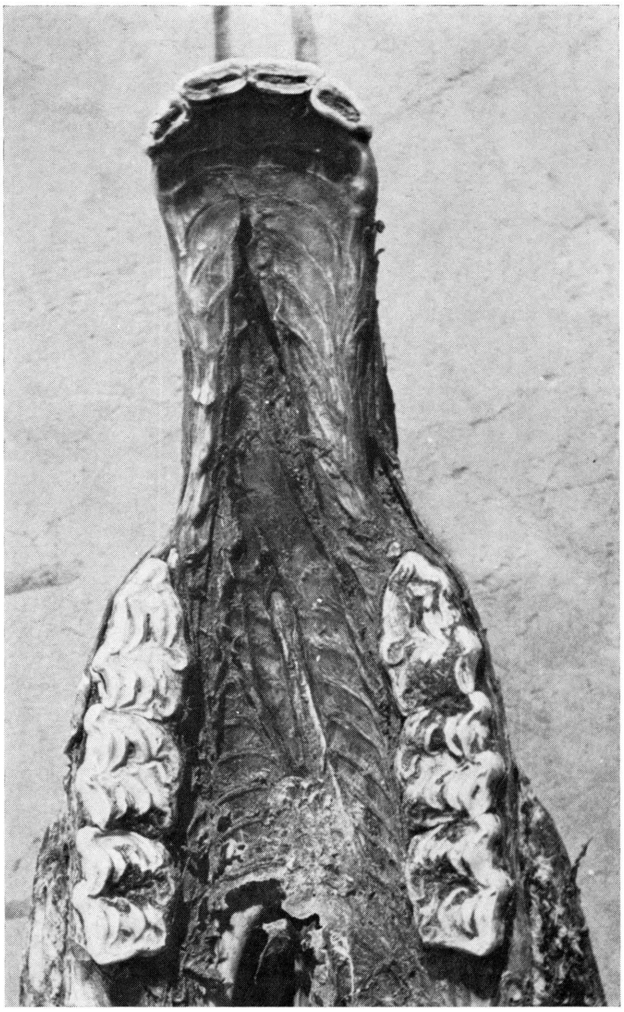


Plate 20: Age class II, one to three months, id_2 erupted and in wear.

Plate 19: Age class I, id_1 erupted and in wear.

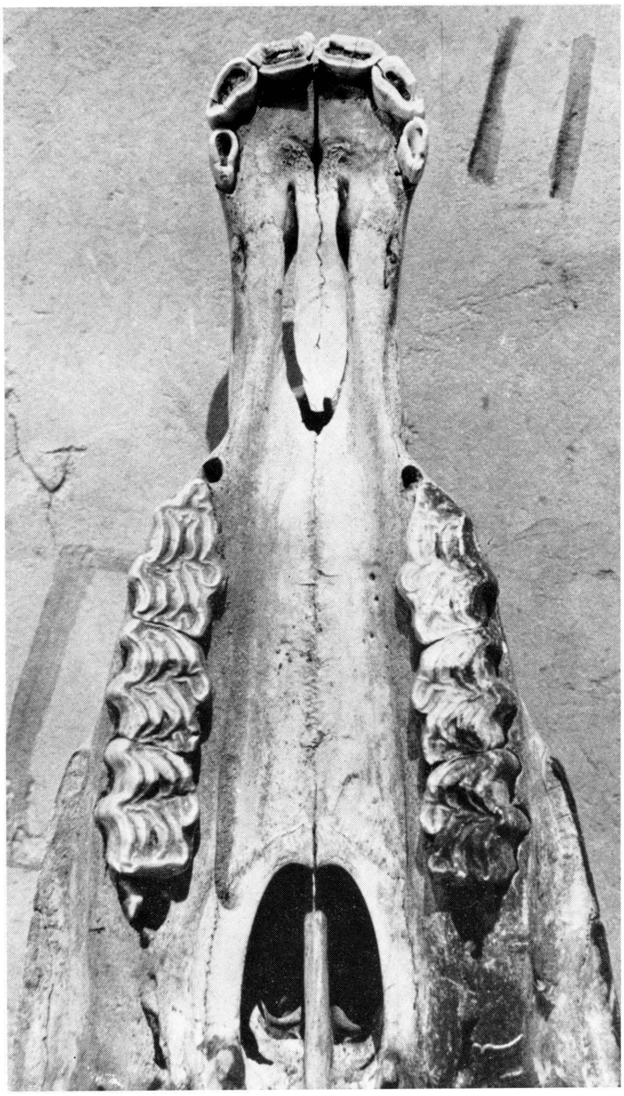


Plate 21: Age class III, six to nine months, id_3 erupted, but not yet in wear.

Plate 22: Age class III, id_3 erupted but not yet in wear.

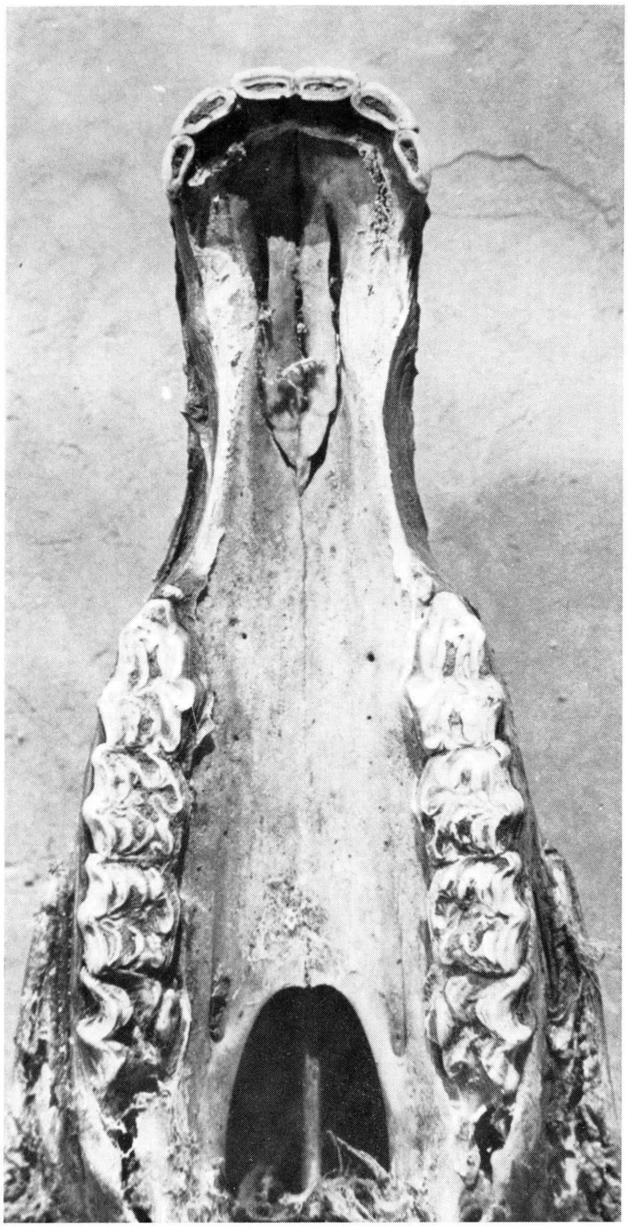


Plate 23: Age class IV, one year, M_1 erupts.

Plate 24: Age class IV, id_3 in wear. Note the prominent necl shown by the milk incisors that is absent in the permanen incisors.

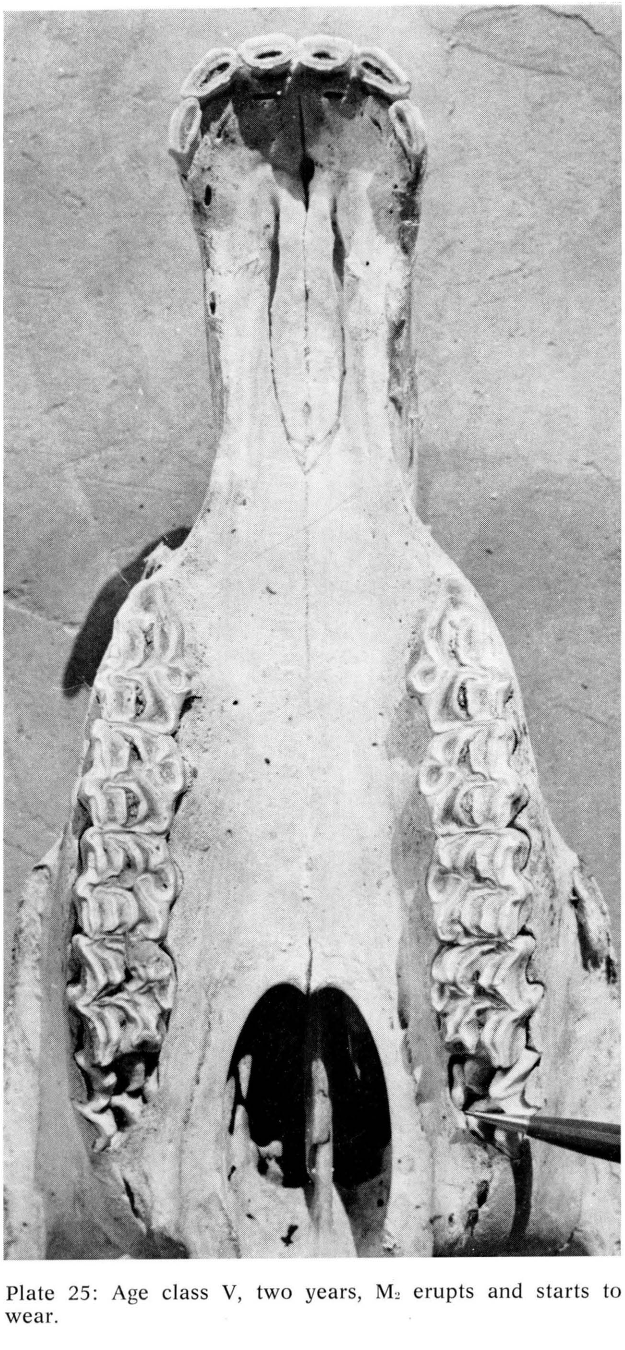


Plate 25: Age class V, two years, M_2 erupts and starts to wear.

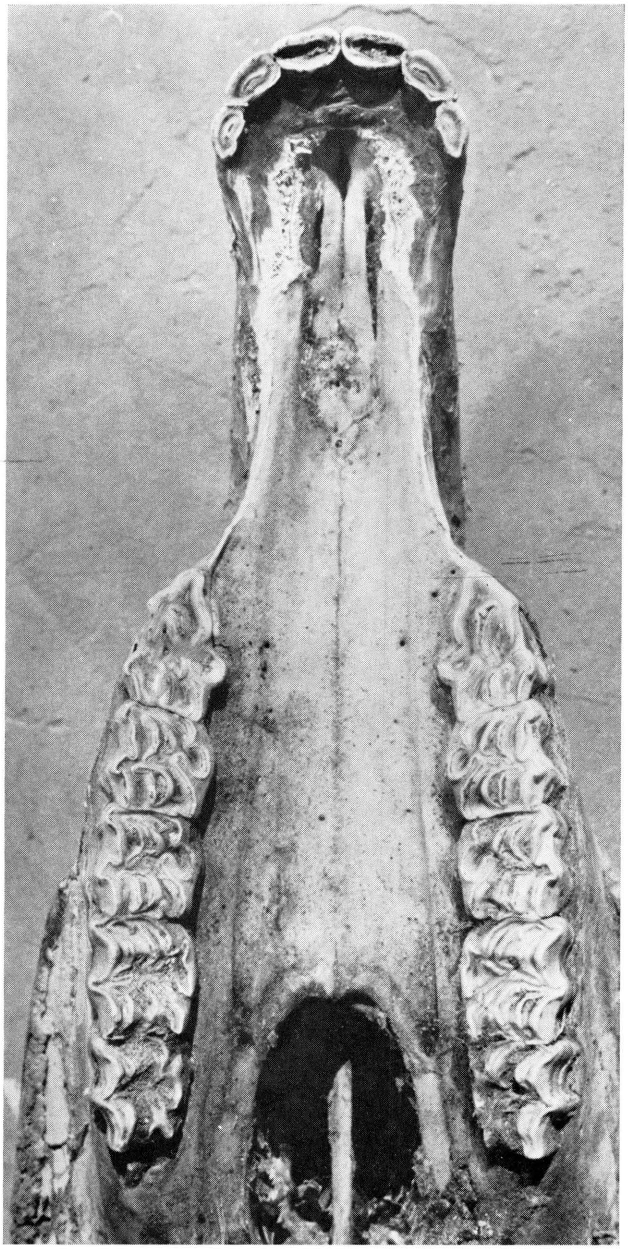


Plate 26: Age class VI, two and a half years.

Plate 27: Age class VI, I_1 replaces id_1, not yet in wear.

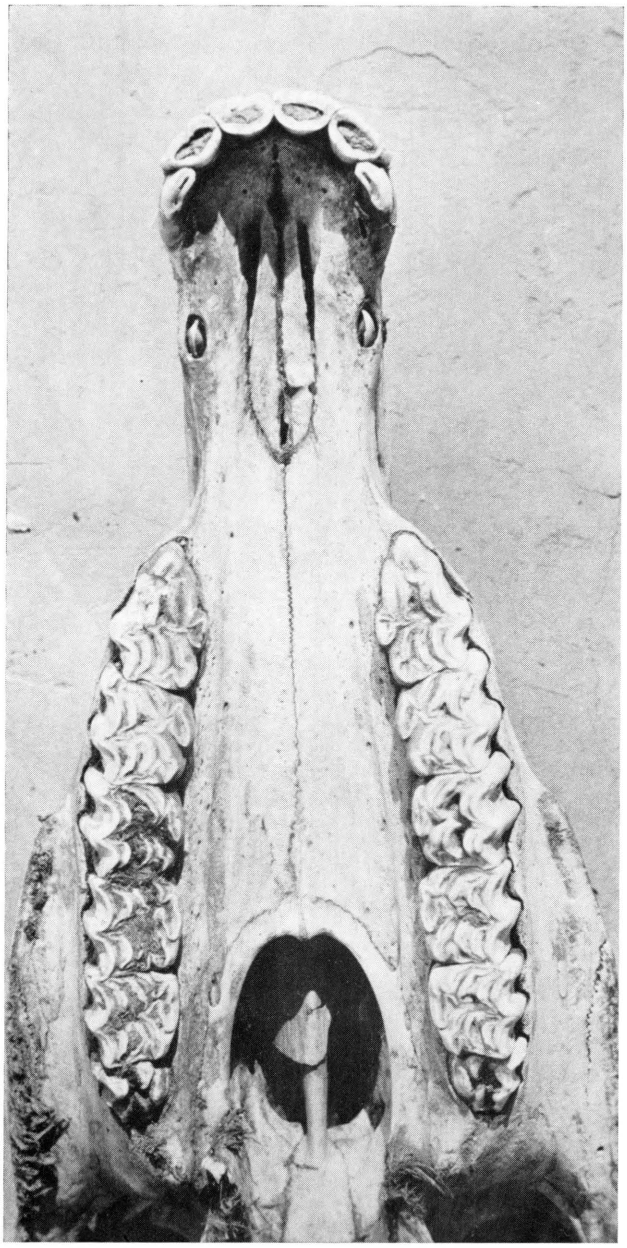


Plate 28: Age class VII, 3 years, M_3 erupts, pd_2 and pd_3 replaced by P_2 and P_3.

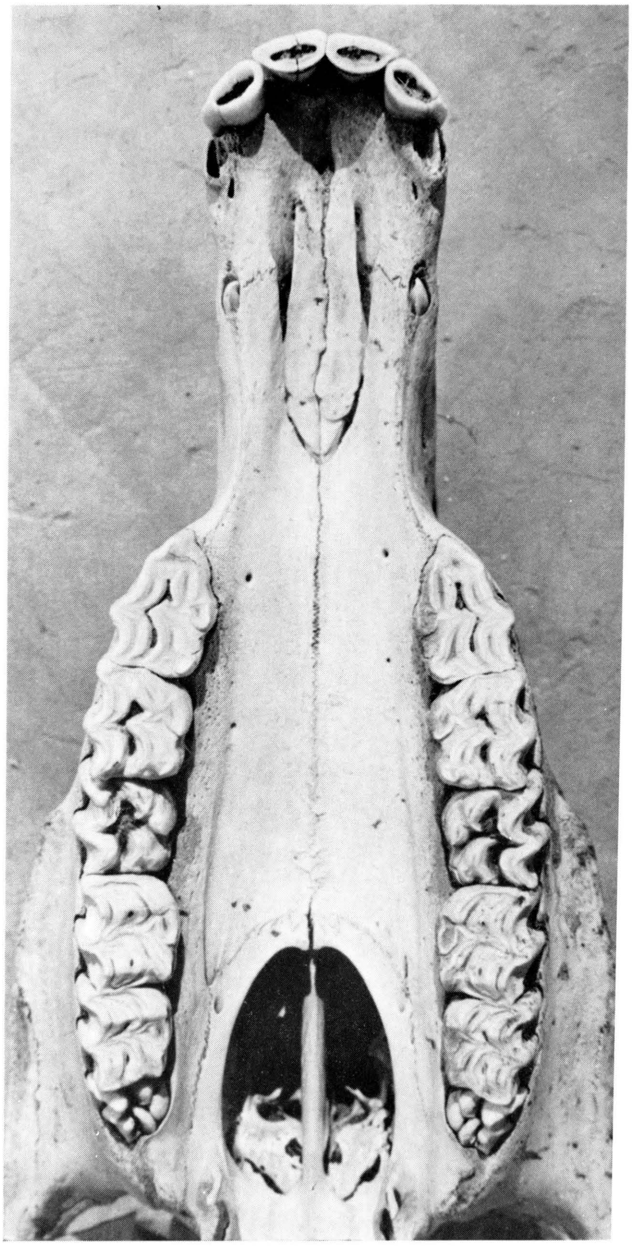


Plate 29: Age class VIII, three and a half years, M_3 starts t wear, pd_4 replaced by P_4.

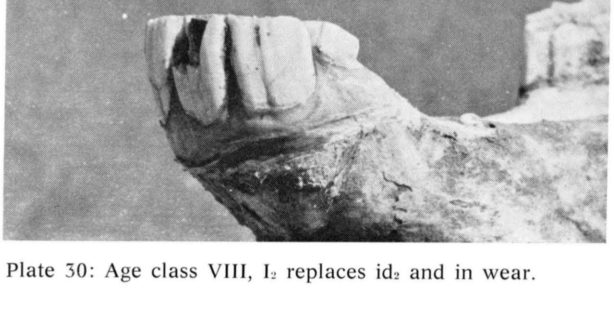


Plate 30: Age class VIII, I_2 replaces id_2 and in wear.

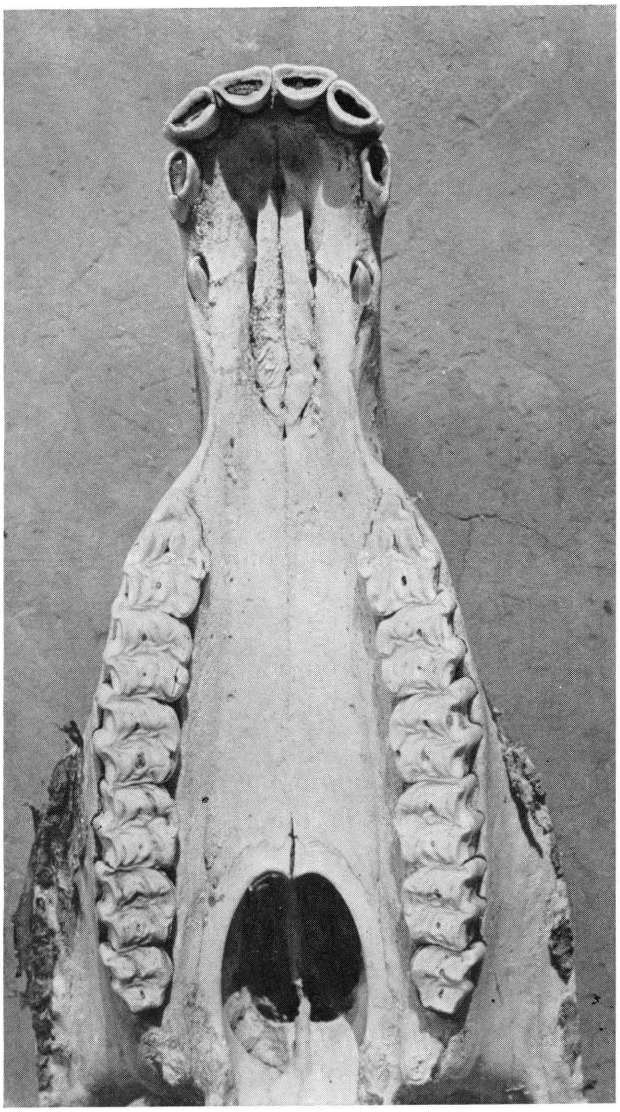


Plate 31: Age class IX, 4 years, M_3 in wear.

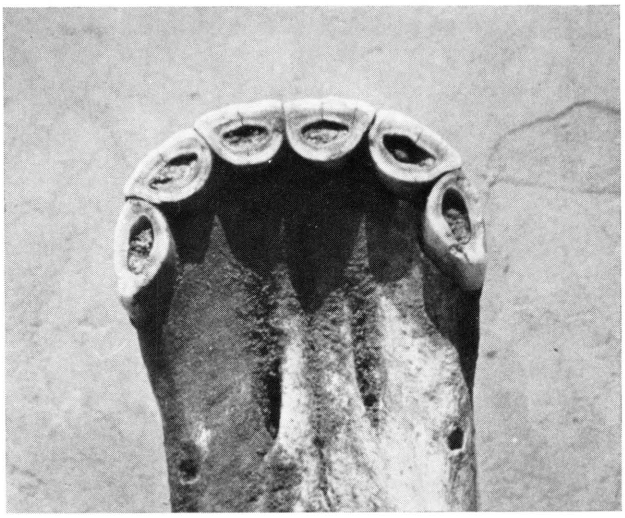


Plate 33: Age class X, 5 to 6 years, I_3 in wear. Infundibula of I_1 oval, of I_2 and I_3 long.

Plate 32: Age class IX, I_3 replaces id_3, not yet in wear.

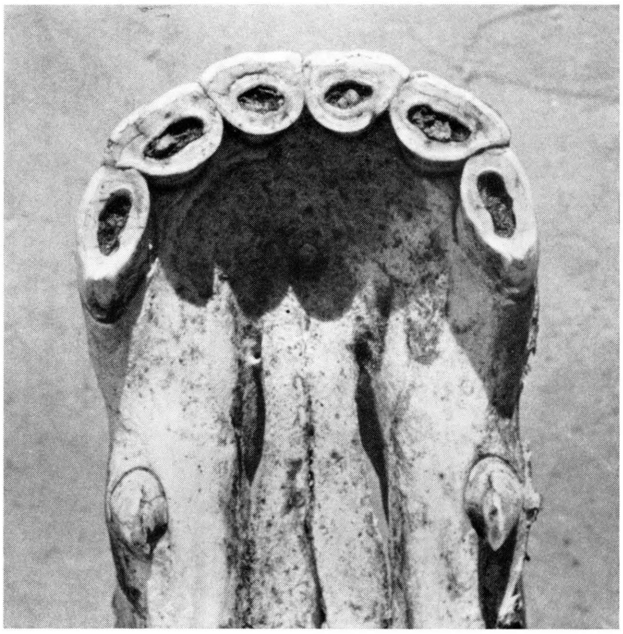


Plate 34: Age class XI, 7 to 9 years. Infundibula of I_1 round-oval, I_2 oval and I_3 long-oval.

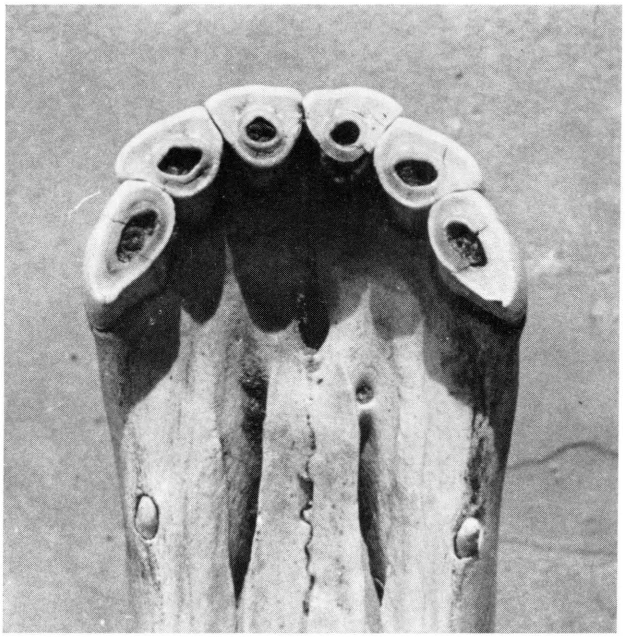


Plate 35: Age class XII, 9 to 11 years. Infundibula of I_1 round, I_2 round oval.

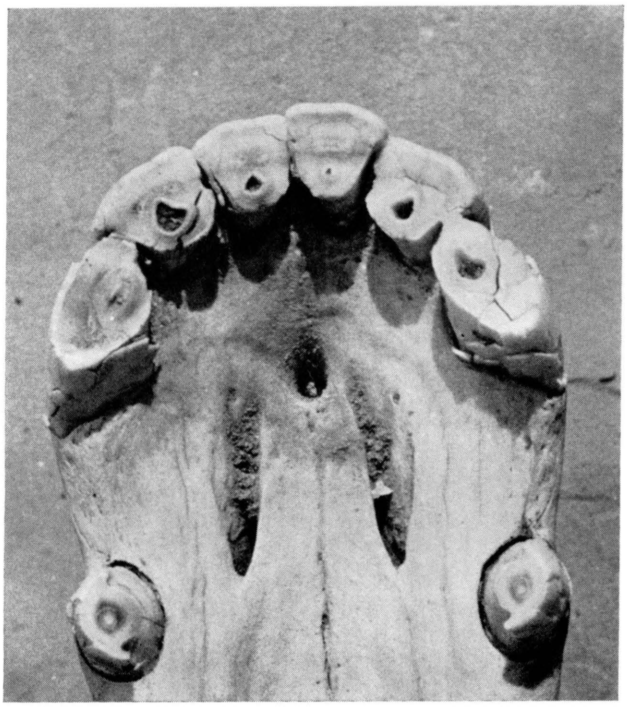


Plate 36: Age class XIII, 11 to 13 years. Infundibula of I_1, absent, 1_2 round.

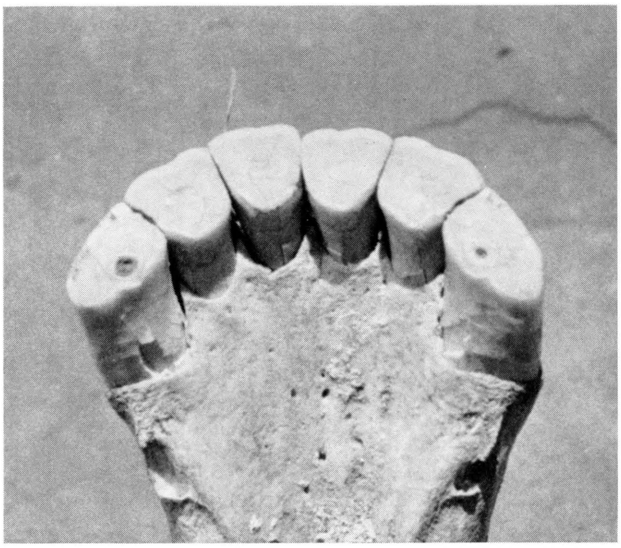


Plate 37: Age class XIV, 12 to 14 years. Infundibula of I_3 small and round.

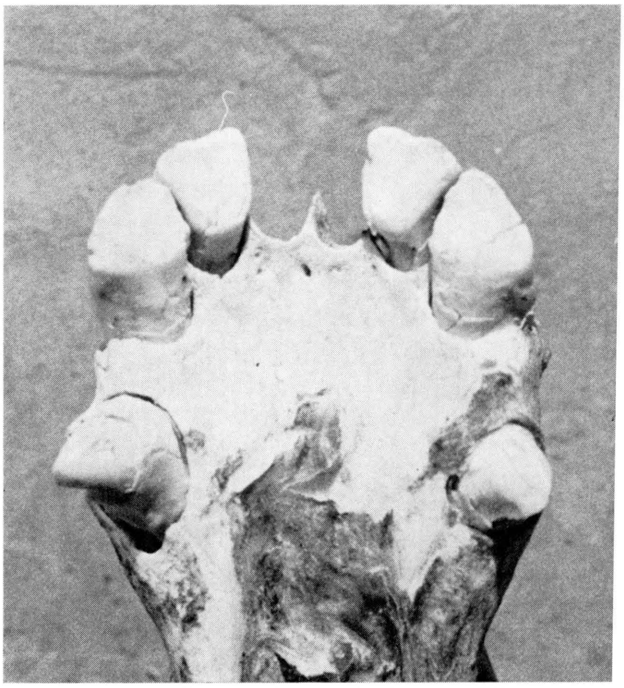


Plate 38: Age class XV, 15 years plus. Infundibula of I_3 absent.

4.4 REPRODUCTION.

In contrast with the domestic horse very little is known about reproduction in zebras. The most comprehensive work in this regard was done by King (1965). In this work he records field work done on Grant's zebra (Equus burchelli böhmi) and Grevy's zebra (Equus grevyi).

4.4.1 Reproduction organs.

4.4.1.1 Males.

The testes are carried externally in the scrotum which hangs betwe the thighs. The scrotum is normally naked except for scattered hairs. The vas deferens passes from each testis, through the inguinal canal to the floor of the pelvic cavity. The accessory organs lie on the ventral floor of the latter cavity. The seminal vesicle opens into the urethra in front of the prostate gland. The urethra passes behind the symphysis pubis into the penis along the ventral surface of the abdomen (King, 1965).

4.4.1.2 Females.

The two ovaries and uterine horns lie within the abdominal cavity, while the uterus, cervix and vagina lie in the pelvic region. The genital tract is suspended from the dorsal wall by a broad ligament, which is a fold of the peritoneum (King, 1965). The ovaries show a variety of shapes according to the stages of differentiation of the maturing follices. Usually, however, they are kidney or pear-shaped.

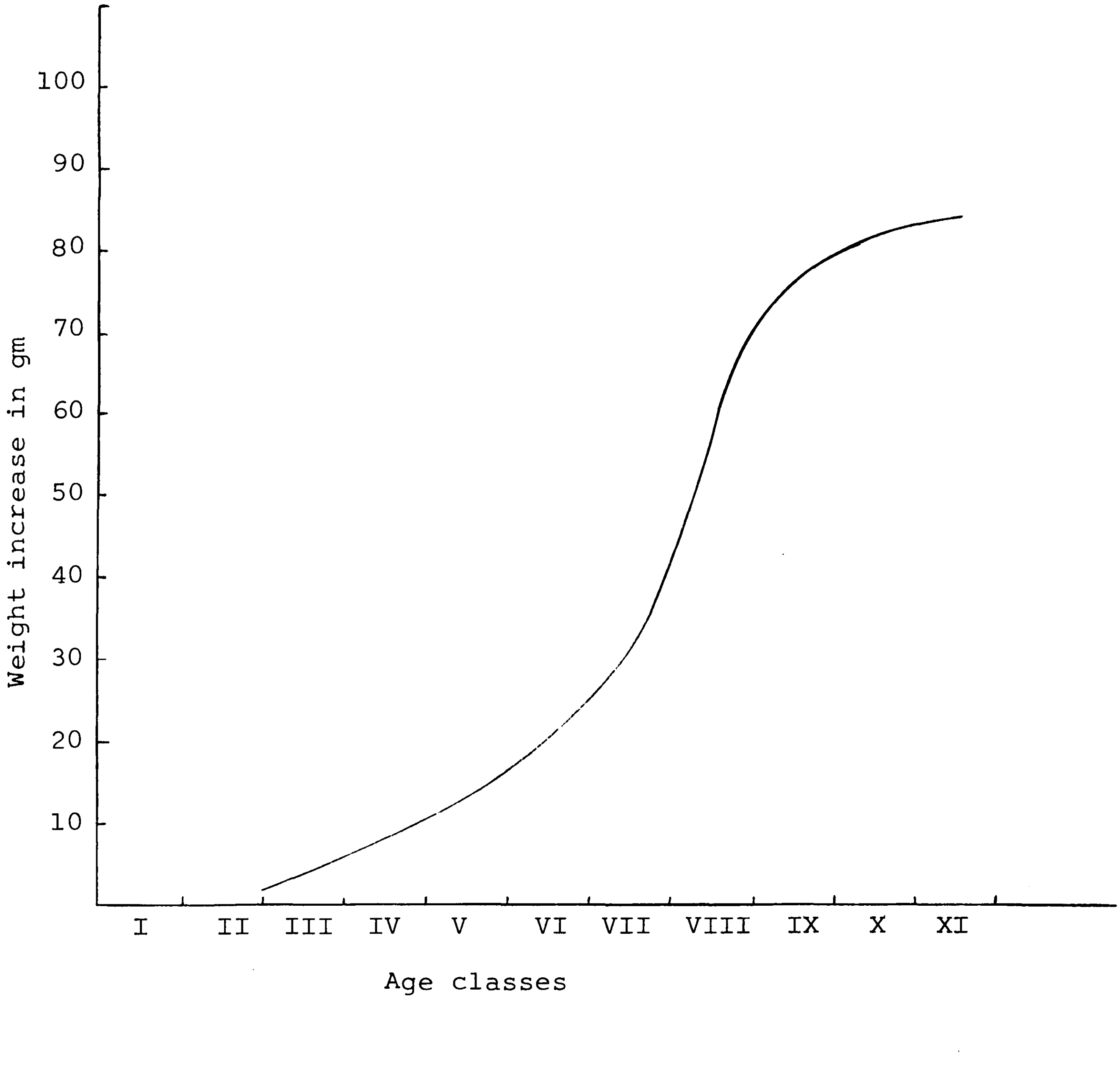
4.4.2 Age when sexually mature.

4.4.2.1 Males.

In the Hartmann zebra, as in the Burchell zebra (Klingel, 1963 and King, 1965) the age at which the male starts showing sexual activity is no indication of puberty. It is only when they are able to compete with

Figure: 4.7.

Increase in testis weight in the *Equus zebra hartmannae*.



older males and succeed in obtaining their own females that they show breeding activity. As can be seen in figure 4.7 the testis of the male starts increasing in weight from approximately two years of age. The testes however, only reach their maximum weight and size at about three and a half years of age.

The average size of the testis (n = 24) of animals older than four years is 6,6 cms x 4,9 cms and the average weight 87,6 gm. This is markedly smaller than the size 10 x 7 x 5 cms given by King (1965) for the Burchell zebra.

From post mortems carried out in the field it looks as though the testes only descend into the scrotum after the animal has reached the age of two and a half years or more.

4.4.2.2 Females.

Klingel (1965) records that the first oestrus of a Burchell zebra mare takes place at 12 to 13 months. Although it might also occur at this age in the Hartmann zebra, no opportunity arose to record this in field observations. Several females of known age dropped their first foal at three years or shortly afterwards. A female collected in the field, at an age of three years, was on the point to giving birth. With a gestation period of approximately 12 months one can therefore assume that in the Hartmann zebra female sexual organs have reached their full development and function normally from about two years of age.

The average weight of 26 pairs of ovaries obtained from breeding females is 47,3 gm. (Maximum 141,53 gm - minimum 19,64 gm). The average length of these ovaries (over the median) is 43,3 mm (maximum 63,6 mm - minimum 31,0 mm).

Cross-section of ovaries of sexually

immature females showed them to be brown on the inside as opposed to the whitish colour of sexually active ovaries.

4.4.3 Reproductive cycles.

4.4.3.1 Males.

To determine reproductive cycles of the male, testes of adult animals were collected. As already mentioned, a number were collected every month throughout one year. The testes were weighed and measured. Smears were made from the epididymis to determine the number of spermatozoa.

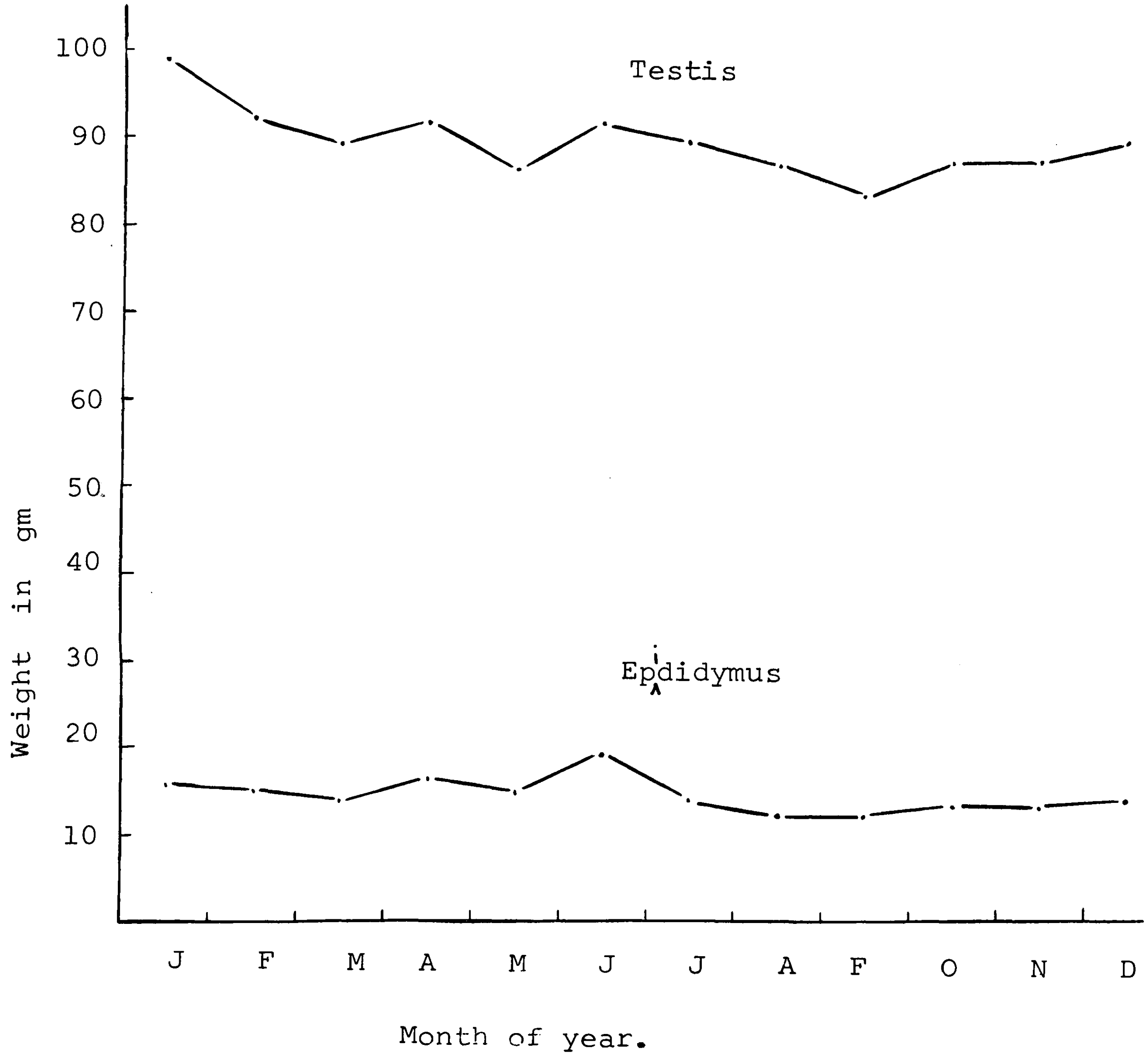
As can be seen from figure 4.8 only a very slight variation in the weight of the testis is noticeable during the 12 months of the year. The average weight of the testis shows a slight decline from a peak in January (99,4 gm) to the lowest point during September (83,1 gm). Semen counts by the S.A.I.M.R during January gave an average figure of 4,600,000,000 spermatozoa per ml, while during September the average figure obtained was 1,900,000,000 spermatozoa per ml. The number of abnormal spermatozoa remained at an average of 9 per cent throughout the year. From the above it would appear as though the testes are more active during the rainy months than during the dry months. Despite this however, there is still more than enough spermatozoa to fertilize a female during the drier months.

4.4.3.2 Females.

Twenty-six pairs of ovaries were collected during the study period. No differentiation in the activities of the ovaries could be detected. Follicles of Graaff were found maturing either in the left, or right or more often both ovaries. Before rupturing, the follicle normally reached such a large volume that it projected beyond the surface of the ovary.

Figure 4.8

Seasonal changes in weight of testis and epididymis in adult <u>Equus zebra hartmannae</u> males.



Sometimes several of these large follicles would be found in one ovary at the same time. Even the number of developing follicles in each ovary showed a marked similarity. The outer walls of these follicles are thin and care had to be taken not to rupture them while working with the ovaries. The average diameter of these maturing follicles was 25,5 mm.

Kupfer (1928) found that donkey and horse mares show a definite periodicity of ovarian activity. Kupfer states that in South Africa, in the animals mentioned above, ovulution takes place only during the months October (second half), November, December, January, February, March and April (first half). Ovulations are thus confined to a season of six or seven months. King (1965) and Klingel (1965) detected no breeding season in Burchell and Grey's zebra in East Africa. Klingel (1965) however, reports a main foaling season from January to March for the Burchell zebra. In the Hartmann zebra new-born foals have been recorded throughout the year, but a distinct breeding peak is also noticeable. This is a clear indication that conception can take place throughout the year. During the three years of study, however, mating activities were only seen from September to April the following year, with a peak in February (for the 3 years of observation). This indicates that mating activity during the rest of the year is very rare. This agrees with the work done by Kupfer (1928) on the donkey and horse to some extent.

One of the marked characteristics found in the ovaries investigated was the presence of a large corpus luteum even at an advanced state of pregnancy of up to five months. King (1965) found the same in the Burchell zebra.

Kupfer (1928 : 1245) reports the same :

> "the whole process of transformation from the ruptured follicle to the yellow body and its reduction, takes a very long time in South African donkeys (and in South African

> equines- horses- altogether) when compared with other animals. A rapid development and reduction of the corpus luteum, such as found in a concentrated ovulation cycle with intervals of three weeks only (for instance cattle) does not take place here."

The average size of the corpus luteum before reduction takes place is similar to that in Burchell zebra as found by King (1965) viz. 25 mm. The colour changes of the corpora lutea were also found to be similar as described by Kupfer (1928) and King (1965). The active corpus luteum has a red-brown colour before changing to yellow.

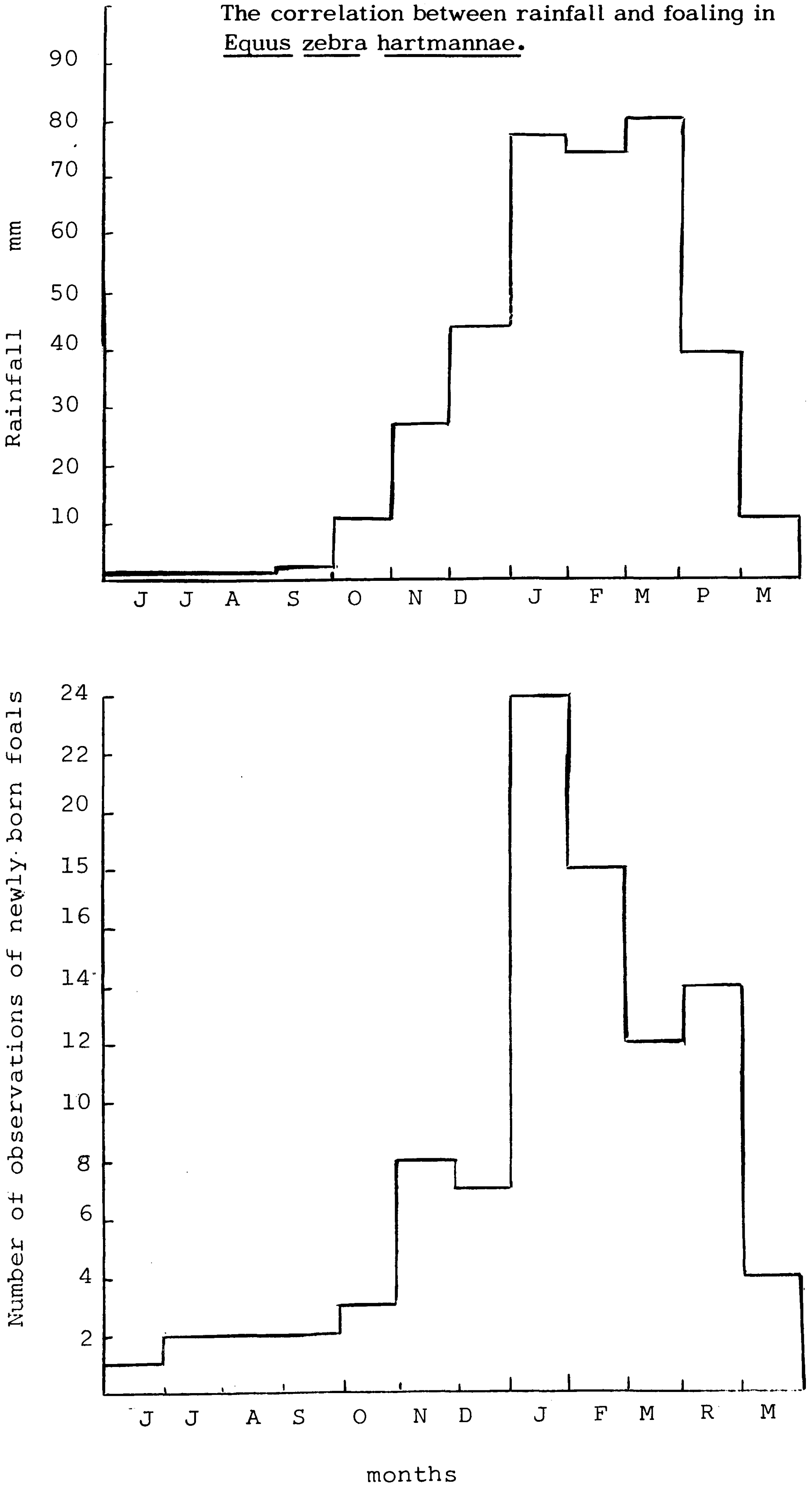
King (1965) found in ovaries 3 to 6 weeks post-partum (n = 4) remnants of a corpus luteum which appeared to be slightly larger than that seen at full term. This was found in one animal's ovaries in Hartmann zebra and suggests oestrus a week after parturition. Oestrus 8 - 10 days post-partum has been observed in both captive (Wackernagel, 1965) and free animals (Klingel, 1965). From observations at the Daan Viljoen Game Reserve the foaling - conception interval varied between three to seven weeks. It appears as though conception does not take place during the first oestrus following parturition.

4.4.4 Season of breeding.

As already mentioned new-born Hartmann zebra foals have been recorded throughout the year. But as Klingel (1965) found in the Burchell zebra a clear peak is noticeable. In the Hartmann zebra this peak is from November to April - thus commencing a month later and ending a month later than what Klingel found in Burchell zebra. This might be attributed to the rainfall season in South West Africa (See figure 4.9). Newly born foals recorded over the three year study were distributed as follows. During November to the end of April 86 per cent of all foals were born (Burchell zebra, October to March = 85.5 per cent), with 68 per cent during the main foaling season January to April (Burchell zebra,

Figure 4.9

The correlation between rainfall and foaling in *Equus zebra hartmannae*.



January to March = 61 per cent).

4.4.5 Gestation period.

Wackernagel (1964) gives the gestation period of Burchell zebra as 371 days. This was determined in a zoo. Only one accurate gestation period could be recorded from the Hartmann zebra. A pair was kept in an enclosure next to the Legislative Building in Windhoek. On the 25th July, 1967, Mr. Holtzhausen saw the pair mating and on the 23rd July, 1968 the female gave birth to a foal. This gives a gestation period of 364 days.

4.5 POPULATION COMPOSITION.

Owing to the social organization, the difficulty of quickly and accurately sexing animals in the field, as well as the habitat the Hartmann zebra frequents, it is virtually impossible to sample a population in the field. Klingel (1965) experienced similar problems with the Burchell zebra, and he gives only the sex ratios of the foals born in marked groups. In their population study on the wildebeest, Talbot & Talbot (1963) faced the same problem.

A reasonably accurate census of the Khomas Hochland population of Hartmann zebra was carried out during the study. The total population was therefore known. From this population (5 000 animals) a random sample of 128 animals was collected. Although this sample represents only 2,5 per cent of the population in the Khomas Hochland the author is confident that the calculations based on these figures must give a picture as nearly accurate as one could hope to get of a wild population.

4.5.1 Sex ratios.

The embryos and foeti collected during the study period, and which could be sexed, showed a male : female ratio of 1 : 1,12 (n = 18). This is a ratio of 47 per cent males to 53 per cent females; it is not significantly different and can be considered equal. The male : female ratio for foals up to the age class VI (two and a half years old) is 1 : 1,08 (n = 57), thus 48 per cent males, a difference which is even less significant than the figure obtained from foeti.

The sex ratios for the various age classes from age class VIII (three and a half years) onwards are given below.

TABLE 4.3

SEX RATIOS OF AN ADULT EQUUS ZEBRA HARTMANNAE POPULATION IN THE KHOMAS HOCHLAND.

Age class.	Age.	Male.	Female.	ratio.	n
VIII	3½ years	1	2	1 : 2	3
IX	4 years	9	12	1 : 1,3	21
X	5 - 6	9	7	1 : 0,7	16
XI	7 - 9	7	10	1 : 1,4	17
XII	9 - 11	4	4	1 : 1	8
XIII	11 - 13	1	0	1 : 0	1
XIV	12 - 14	0	1	0 : 1	1
XV	13 - 16	1	1	1 : 1	2
Total		32	37	1 : 1.16	69

As can be seen, the sex ratios in the various age classes vary; despite this, the sex ratio of the entire sample of adult animals is 1 : 1.16 - still insignificant. One of the reasons for this almost equal distribution of sexes in the adult animals must be the lack of conspicuous dimorphism between the sexes. It also shows that both sexes are equally well adapted to their environment.

4.5.2 Age structure and dynamics.

As Allee et al (1949) put it a population has certain characteristics it shares with an organism as well as others that are its own unique possession. The latter group of characteristics are largely statistical. Statistical methods have been developed for the analysis of human populations. These methods have been adapted with considerable success to wildlife management.

In the analysis of population dynamics the numerical and structural changes within population resulting from births, deaths and movements must be considered Quick (1963). For this paper, only the Khomas Hochland population of Hartmann zebra will be discussed. This population is for all practical purposes stable.

As has already been mentioned 128 animals were collected on a random basis in the field. This sample was grouped into the various age classes, using tooth development and wear as parameters. The result obtained can be seen in table 4.4

TABLE 4.4

DISTRIBUTION INTO AGE CLASSES OF A RANDOM SAMPLE OF EQUUS ZEBRA HARTMANNAE COLLECTED IN THE KHOMAS HOCHLAND.

Age class.	n	Age groups.	Total.
I	10		
II	3		
III	6		
IV	8	1 year	27
V	15		
VI	15	2 years	30
VII	2		
VIII	3	3 years	5 (+30)*
IX	21	4 years	21
X	16	5 - 6 years	16
XI	17	7 - 9 years	17
XII	8	9 - 11 years	8
XIII	1	11 - 13 years	1
XIV	1	12 - 14 years	1
XV	2	15 years and over	2
		n =	128

*Correction factor for the determination of a life-table - see text.

This sample, as has already been mentioned, was collected at random (helped to a large extent by the absence of sexual dimorphism in the Hartmann zebra). It was also possible to indentify the animals into more than two age-classes - thus fulfilling the two basic prerequisites for the application of a life-table method of population analysis. To obtain more even intervals between the age classes, several of them were grouped together in age groups (see table 4.4). As can be seen only 5 individuals of age classes VII and VIII were collected. This was at first thought to be due to certain defects in the method of sampling. As can be seen in figure 4.10, however, this corresponds to a drought period in the Khomas Hochland which had an adverse effect on the survival rate of foals during that year (See Limiting factors). A graph was plotted with the information in table 4.4 and smoothed out to give the theoretical figure for the age group: three years.

An age structure curve and life table were then constructed (Quick, 1963). To determine the number of foals born, the following procedure was used. The total population of _Equus_ _zebra_ _hartmannae_ on the Khomas Hochland numbers 5,000. Using the information in table 4.3 it follows that 54 per cent of the population must be females. Assuming that theoretically 1675 mares of three years and older, dropped foals in a given year (1970), this gives one a figure of 33 per cent foals in the population. According to the sample collected in the Khomas Hochland however, one year old foals formed only 21 per cent of the population. Thus 12 per cent of the foals succumbed during their first year.

re 4.10.- Population survival: ~~curve~~ illustrating the influence of a po rainy season on a *Equus zebra hartmannae* population in the Khomas Hochland.

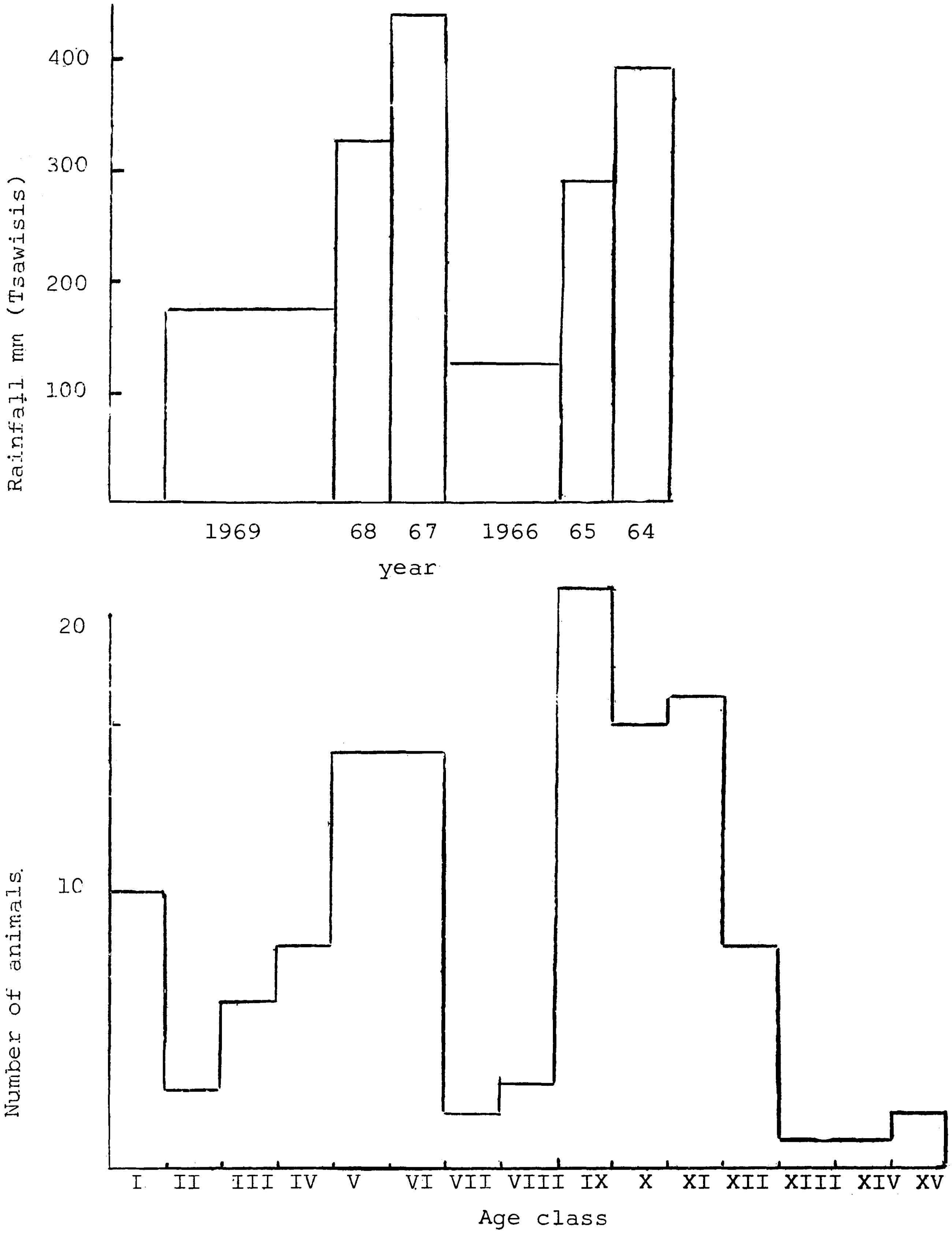


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TABLE 4.5

LIFE-TABLE FOR THE EQUUS ZEBRA HARTMANNAE POPULATION IN THE KHOMAS HOCHLAND.

(Age class) x	I_x	d_x	q_x	*L_x	e_x
0	5000	608	608	4696	3.56
1 year	4392	750	854	4017	2.98
2 year	3642	835	1147	3224	2.49
3 year	2807	973	1733	2320	2.09
IX	1834	583	1484	1542	1.93
X	1251	445	1779	1028	1.61
XI	806	472	2928	570	1.22
XII	334	223	3339	222	1.25
XIII	111	29	1219	96	1.74
XIV	82	26	1342	69	1.18
XV	56	56	5000	28	0.5

* Fractions are ignored.

The life-table above was based on a cohort of 5,000 and is thus directly applicable to the Khomas Hochland population. The headings are those commonly used in basic life-table calculations (Allee et al, 1949). They are :

x - age in appropriate units, stated as an interval;

I_x - the number surviving at the beginning of the age interval stated in the x column;

d_x - the number dying within the age interval stated in the x column;

q_x - the number dying in the age interval divided by the number of survivors at the beginning of the interval, viz. the rate of mortality;

L_x - is the mean number of individuals alive between the stated age - classes;

e_x - life expectation, mean length of life remaining to each organism alive at the beginning of the age class, expressed in terms of age classes.

As can be seen by the age-specific mortality rates q_x, as well as the age structure curve, the survival rate for foals is quite high. This is in strong contrast with what Talbot and Talbot (1963) found in the wildebeest, but in agreement with Klingel's (1965) findings in the Burchell zebra. Up to three years of age the Hartmann zebra foals have a relative high life expectancy. This is probably due to the protection offered to the young by the breeding units.

4.6 LIMITING FACTORS.

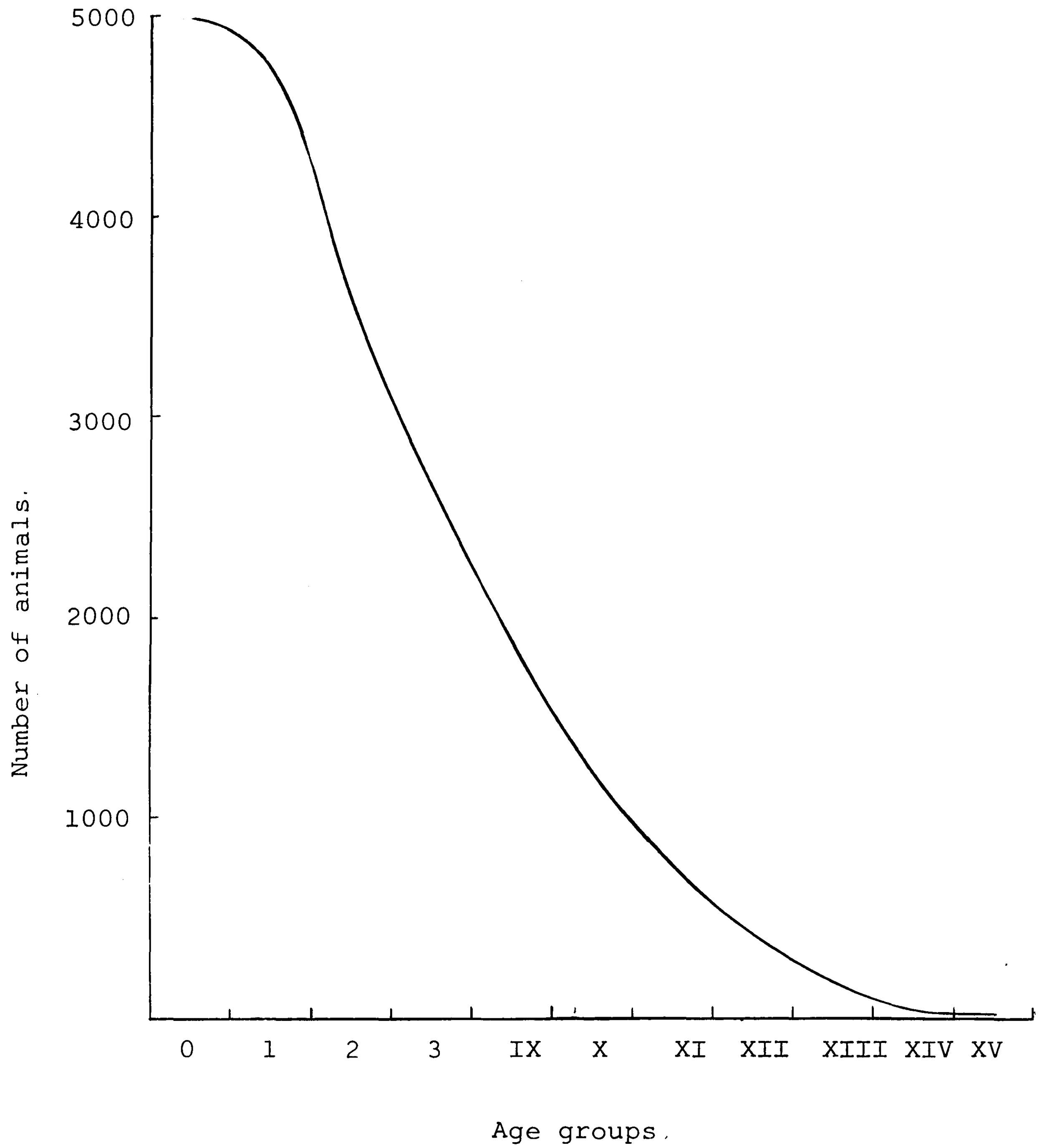
Owing to the broken terrain it was found extremely difficult to record mortalities in the field. Although no accurate figures are available, certain limiting factors were determined during the study period. These limiting factors are drought, accidents, predation and possibly parasites and diseases.

4.6.1 Drought.

Although drought occurs only at irregular intervals and with variable intensity it is one of the primary causes of known mortality. During the drought of the 1968/69 season hundreds of Hartmann zebra were found dead or dying in the Khomas Hochland. At three dry waterholes in the Kuiseb River 32 carcasses were found. On another farm in the Khomas Hochland, 21 carcasses were found of animals that had been trapped in the mud of a dam drying up.

Figure 4.11:

Age-Structure curve for a population of *Equus zebra hartmanae* in the Hochland.



Normally the heavily hunted Hartmann zebra on the Khomas Hochland are very wild and shy and will make off whenever they spot a vehicle. During this abovementioned drought however, they wandered aimlessly around, especially around dried up waterholes and along the Kuiseb River. One could drive to within fifty yards of them. The farmers, who during this time were also hard hit, mercilessly shot hundreds of Hartmann zebra. The primary cause for this was that these animals were in direct competition with the livestock, not only for water, but also for grazing. A second factor was that during this period, untanned zebra hides fetched prices of up to R35 apiece; that of young foals even more. Zebra hides thus ensured a ready cash income for the farmers.

The heaviest mortality in the Hartmann zebra population during this drought, occurred amongst the newly-born to young foals and pregnant females. Strange as it may seem a dead or dying female was found on several occasions with her young (new-born to a few months old) foal standing next to her. This might be due to the drain of lactation on the female and a shortage of food. In animals weighed during December 1969/January 1970, at the height of the last drought, it was found that the contents of their digestive systems formed only 12 per cent of their body weights. In animals weighed from July 1970, onwards, after good rains had fallen, the contents of their digestive systems formed 25.4 per cent of their body weights.

Post mortems on three females also revealed signs of recent abortions. No aborted foeti, however, were found in the study area - probably because they were quickly disposed of by scavengers. Mr. B. de la Bat (pers. com. 1970) informed the author that he recorded several aborted Burchell zebra foeti during severe droughts in the Etosha National Park.

4.6.2 Accidents.

Considering the habitat they frequent it is not surprising that accidents also cause mortality, especially among the adult population. Although no figures are available from the field, eight per cent of the population at the Daan Viljoen Game Reserve died owing to accident during 1969 and 1970. Several deaths owing to accidents were also recorded by P. van der Westhuizen (5) and W. Piepmeyer (2) (pers. com. 1969, 1970) from the Naukluft Mountain Zebra Park. Several carcasses with fractured bones were found under various precipices.

As already stated adults, male and female alike, are most accident prone. Accidents normally occur during play-fighting or maintenance of social hierarchy activities; probably also when fleeing from danger, real or imagined, especially around waterholes. The most common injuries are fractures of the legs and although not the actual cause of death they form the primary factor that leads to the animals' death.

4.6.3 Predation.

In the Khomas Hochland predators such as leopard (Panthera pardus) and cheetah (Acinonyx jubatus) are still relatively common. Although they may not have a marked influence on the population they certainly remove a certain percentage, especially of foals. At one very secluded waterhole in the Naukluft mountains on the farm Panorama, a large number of skeletons of primarily young animals lie scattered around. Some of them were relatively fresh, and although cause of death could not be ascertained, it seemed very likely that it was due to predation. On the same farm, the owner, Mr. Visagie, told the author that during the last 10 years they lost almost 75 per cent of their horse and donkey foals to predators.

In the Namib Desert Park, in the Kaokoveld and the area to the west of Otjovasandu, hyenas (*Crocuta crocuta*) and wild dogs (*Lycaon pictus*) also assist in reducing the population. During 1967/68 three deaths owing to predation by lion (*Panthera leo*) were recorded by the author in the Otjovasandu area.

4.6.4 Parasites and diseases.

Hartmann zebra, as Burchell zebra, are heavily infested with internal parasites. Apparently however, these parasites have no real detrimental effect on the animals. During years of severe drought however, the internal parasites are bound to have a certain adverse effect.

Internal parasites recorded are the following:

Gasterophilus pecorum (Fabt.)
G. ternicinctus Ged.
Rhinoestrus steyni
G. intestinalis (De Geer).
G. haemorrhoidalis

External parasites are mainly ticks situated in the scrotal area. No heavy infestations were ever found.

Ticks recorded are the following:

Rhipicephalus oculatus Neumann
R. evertsi ssp. *mimeticus* Dönitz
Hyalomma rufipes Kock

A new louse was also found from material collected during the study. This louse belongs to the *Damalinia*, but has not yet been described.

There is no record whatsoever of Hartmann zebra dying of any diseases. Death due to disease in nature, however, is difficult to establish. In the Etosha National Park, anthrax annually kills a number of animals especially Burchell zebra. In the Otjovasandu area, despite strict vigilance, the collection of blood smears from all fresh carcasses, not one death due to anthrax was recorded in the Hartmann zebra population.

SUMMARY.

1. The Hartmann zebra in South West Africa is an endangered species as well as a 'problem animal'. A research project was launched to determine its distribution, status, habitat preferenc ecology, behaviour and population dynamics. The results will be used to determine a policy to ensure its survival as well as satisfy the farming community.

2. The physiography of its distribution area and its habitat preference are discussed. The vegetation of the Khomas Hochland is analysed and divided into four physiognomic groups:

riparian vegetation
highland savanna
escarpment vegetation
pre-Namib vegetation.

3. It was found that the main distribution area of the Hartmann zebra is situated in the Khomas Hochland. Other distribution areas are the northern concentration which includes the area to the north of the Ugab River; the Erongo mountains; and th southern concentration in the Huns mountains and the Fish River.

4. An aerial census was carried out during 1968, which covered the whole area from the Orange River in the south to the Kunene River in the north. The total number of Hartmann zebra i South West Africa according to this survey is approximately 7,000

5. The influence of climate on the behaviour of the Hartmann zebra was determined. Temperature and rainfall cause the most marked changes in their activities. Orientation of the body surfaces towards or away from the sun is an important adaptation. Insects cause considerable irritation during the summer months.

6. The digestive abilities of the Hartmann zebra were determined by an experiment in which they were fed lucern hay. The results indicate that there are no marked differences in the ability to utilize hay between the Hartmann zebra and the domestic horse.

7. Blood and urine samples show that the Hartmann zebra does not possess any outstanding kidney function.

8. The social system of the Hartmann zebra is based on two distinct groups; the breeding unit and the bachelor unit. In the breeding unit one finds an exclusive one - male dominance over a given number of females and a characteristic social hierarchy among the females. This social hierarchy amongst the females is considered to be one of the bonds binding the breeding unit. The breeding unit is very stable, the females staying with it all their adult life while the males are replaced when injured or senile.

9. Bachelor units are mainly formed by immature males and most of them become sexually mature during the time of their association with the bachelor group. While in this group selective pressure comes to bear - only the more worthy males acquiring their own breeding unit. Bachelor units function thus both as a natural selector for the best males as well as male reservoirs for replacing dominant males which become senile or die.

10. The important role ritualization plays in the social organization of the Hartmann zebra is discussed. It is not only important in mood transmission but also to suppress fighting; and to unite the group as an independent entity.

11. The principles of behaviour shown by the dominant male are discussed at great length. It is shown that the herding behaviour of males is an innate activity pattern. This innate herding drive by the dominant male is in an inverted ratio to the number of females in the breeding unit.

The relationship between dominant males of various breeding units bears a certain resemblance to a territorial social system. A periphery effect is obtained when two breeding units come close enough to trigger the challenge rituals between the dominant males. The challenge ritual is analysed.

12. The daily activity patterns for various activities; social, comfort and nutritional are discussed.

13. During the study 128 animals were shot on a random basis and th population dynamics worked out. Schedules for pre- and post-natal development are discussed. Based on tooth development, replacement and wear, 15 age classes are determined.

14. In the Hartmann zebra females the sexual organs have reached their full development at two years of age and the female normally drops her first foal at three years of age. A distinct breeding peak from November to April was found to exist.

15. The population composition of the Hartmann zebra is discussed; this includes sex ratios for the various age classes, age structure and dynamics of the population. An age structure curve and a life table are constructed.

SAMEVATTING.

1. Die Hartmann-sebra word in Suidwes-Afrika beskou as beide 'n bedreigde species sowel as 'n probleemdier. 'n Navorsingsprojek is begin om hulle verspreiding, status, habitatsvoorkeur, ekologie, gedrag sowel as populasiedinamika te bepaal. Die resultate van hierdie projek sal gebruik word om 'n beleid te formuleer wat die Hartmann-sebra se voortbestaan sal verseker sowel as die boeregemeenskap tevrede sal stel.

2. Die fisiografie van hulle verspreidingsgebied sowel as hulle habitatvoorkeur word bespreek. Die plantegroei van die Khomas-Hochland word ontleed en in vier plantegroeigemeenskappe verdeel:

oewerplantegroei
hoogland savanna
eskarpementplantegroei
voor-Namib plantegroei.

3. Dit blyk uit die studie dat die hoofverspreidingsgebied van die Hartmann-sebra in die Khomas-Hochland geleë is. Ander verspreidingsgebiede is die noordelikke konsentrasiestreek wat die hele gebied noord van die Ugabrivier insluit, die Erongoberge en die verste suidelike konsentrasie gebied in the Hunsberge en die Visrivier.

4. Met 'n lugsensus wat uitgevoer is tussen die Oranjerivier en Kunenerivier is bepaal dat daar nog 7,000 Hartmann-sebra in Suidwes-Afrik oor is.

5. Die invloed van klimaatsfaktore op die gedrag van die Hartmann-sebra is ook bepaal. Temperatuur en reënval is die twee belangrikste fisiese eienskappe in die ekologie van die Hartmann-sebra. Die orientasie van die liggaam ten opsigte van die son is 'n belangrikke aanpassing. Insekaktiwiteit is 'n bron van irritasie gedurende die somermaande.

6. Met 'n eksperiment in die Daan Viljoen Wildtuin is hulle vermoeë om lusernhooi te verteer bepaal. In 'n vergelyking met dié van perde is gevind dat die Hartmann-sebra se verteringsvermoeëns nie merkbaar verskil van dié van perde nie.

7. Met die ontleding van bloed- en urinemonsters is bepaal dat die Hartmann-sebra net 'n gemiddelde nierfunksie besit.

8. Die sosiale stelsel van die Hartmann-sebra is gebaseer op twee groepe naamlik die aanteeltrop en die vrygeseltrop. Die aanteeltroppe het 'n eksklusiewe, een-hings-dominansie oor 'n gegewe aantal merries. 'n Streng sosiale hierargie bestaan tussen die merries van 'n aanteeltrop. Hierdie sosiale hierargie van die merries word beskou as een van die faktore wat 'n aanteeltrop bind. Die aanteeltroppe is baie stabiel en 'n merrie mag haar hele volwasse lewe in slegs een trop slyt. Die dominante hings word vervang wanneer hy homself beseer of as hy te oud raak.

9. Die vrygeseltroppe bestaan hoofsaaklik uit jong hingste wat gedurende die tydperk van assosiasie met 'n vrygeseltrop geslagryp raak. Selektiewe druk gedurende hierdie stadium verseker dat slegs die beste hingste met hulle eie aanteeltroppe begin. Vrygeseltroppe funksioneer dus as 'n eenheid waar natuurlike seleksie vir die beste hingste plaasvind sowel as a reservoir vir die vervanging van dominante hingste, sou omstandighede dit vereis.

10. Die belangrike rol wat ritualisasie in die sosiale organisasie van die Hartmann-sebra speel, word bespreek. Dit is nie slegs belangrik in die oordrag van stemmingsgevoel nie maar dien ook vir die onderdrukking van gevegte, om die trop te verenig as 'n onafhanklike eenheid teen ander troppe.

11. Die beginsels van die gedrag van die dominante hings in die aanteeltrop word breedvoerig bespreek. Daar word aangetoon dat die 'tropvormings-gedrag' van die hings 'n ingebore gedragspatroon is. Die

intensiteit van 'tropvormings-gedragspatroon' van die dominante hings is omgekeerd tot die getal merries in die aanteeltrop. Die gedragspatroon tussen die dominante hingste van verskillende aanteeltroppe toon sekere ooreenkomste met 'n territoriale sosiale stelsel. 'n 'Periferie-effek' word verkry wanneer twee aanteeltroppe nagenoeg aan mekaar kom om die Uitdaag-ritueel ' tussen die dominante hingste te veroorsaak. Hier ritueel tussen die dominante hingste word ontleed.

12. Die daaglikse aktiwiteitssiklusse vir verskillende gedragspatrone onder andere sosiale en voedingspatrone word bespreek.

13. Tydens die navoringsprojek is 128 diere op 'n ewekansige basis geskiet. Op grond van gegewens verkry is die populasie-dinamika vir die Hartmann-sebra uitgewerk. Voor- en na-geboortlike ontwikkeling word bespreek. Op grond van die ontwikkeling, wisseling en die slytasie van tande word 15 ouderdomsklasse bepaal.

14. Die Hartmann-sebramerrie raak geslagryp op 'n ouderdom van twee jaar. Sy skenk geboorte aan haar eerste vul gewoonlik op 'n ouderdom van drie jaar. Vanaf November tot April vind die meeste aanteelaktiwiteite plaas.

15. Die populasiesamestelling van die Hartmann-sebra word bespreek op grond van geslagsverhoudings vir die verskillende ouderdomsgroepe, ouderdomsamestelling en dinamika van die populasie. 'n Ouderdomsameste lingskurwe en 'n lewenstabel word opgestel.

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