

# The Social Organization and Associated Behaviour in the Hartmann Zebra

## *Equus zebra hartmannae*

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## I. INTRODUCTION

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 group 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 re-



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

present 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.

## II. METHODS

### 2.1. 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.

#### 2.1.1 The Etosha National Park

The only region in the Etosha National Park where Hartmann zebra occur is at Otjovasandu, in the extreme western part of the game reserve. Otjovasandu lies on the 1400 m contour at the fringe of the Hartmann zebra's distribution on 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 Odenaal Commission's proposals, the new western boundary runs five km 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 attention.

- (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.

#### 2.1.2 The Daan Viljoen Game Reserve

This game reserve is situated in the eastern region of the Khomas Hochland at an approximate altitude of 1500 m. By road it is about 28 km 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 was 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.

### 2.1.3 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 region.

This area is populated by approximately 1 000 Hartmann zebra but was visited less frequently than the other areas for behavioural studies.

### 3.1.4 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 km by 60 km. This game reserve was also visited frequently in order to compare the behaviour of these animals with those in the Daan Viljoen Game Reserve.

## 2.2 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 km, 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 cm 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.

## 2.3 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. 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. Social behaviour was observed and noted throughout the observation period.

### III. CHARACTERISTICS OF THE HARTMANN ZEBRA SOCIAL SYSTEM

In the social organization of *Equus burchelli* and *Equus zebra hartmannae* one finds 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 overpopulation 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 organization 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 prerequisite 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.

### IV. 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.

#### 4.1 Composition of sex and age classes in the breeding unit

This aspect will be more fully dealt with in a paper on their population dynamics (Joubert, in press). Figure 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 consists of five individuals. In 53.9 per cent of the observations the numbers vary between four and six, while 65.2 per cent varies be-

tween 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.

Table 1. Age ratios of *Equus zebra hartmannae* in South West Africa.

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

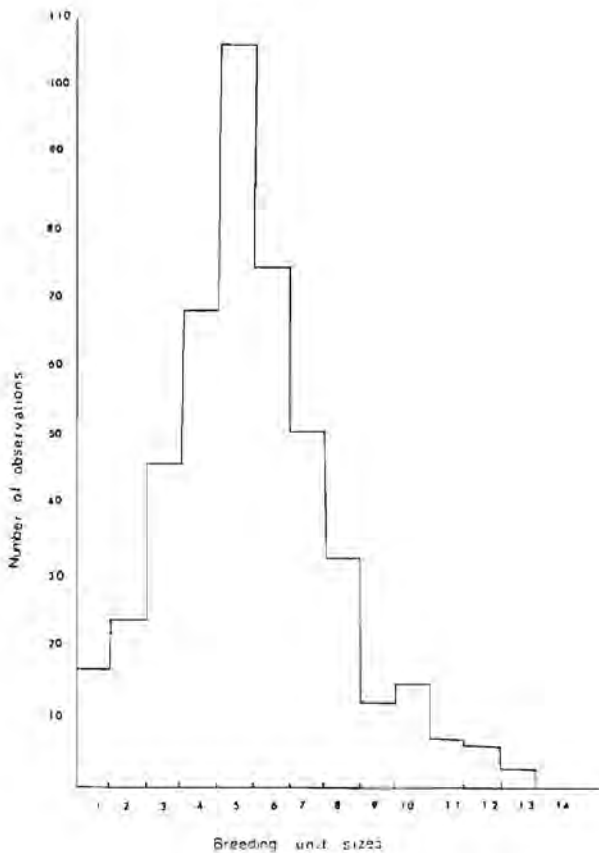


Fig. 1. Distribution of breeding unit sizes for *Equus zebra hartmannae* in South West Africa.

Klingel gives no indication as to age classes. Field studies on the Hartmann zebra produced the following age distribution, as shown by table 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, in the adult animals male: female ratio was also found to be similar. It seems therefore that approximately 50 per cent of the males are in bachelor-unit reservoirs.

#### 4.2. 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 second association is that between the various females and the dominant male, whilst a third type of 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 male's 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.

#### 4.3 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 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 seem 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 initiators 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 exception to this was observed. Quote from field notes:

Daan Viljoen Game Reserve  
Breeding unit 6.

Date:  
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 some one 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 abovementioned 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 apparently 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.

#### 4.4 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 enlargement of existing small ones. This is discussed in greater detail under "formation of new breeding units."

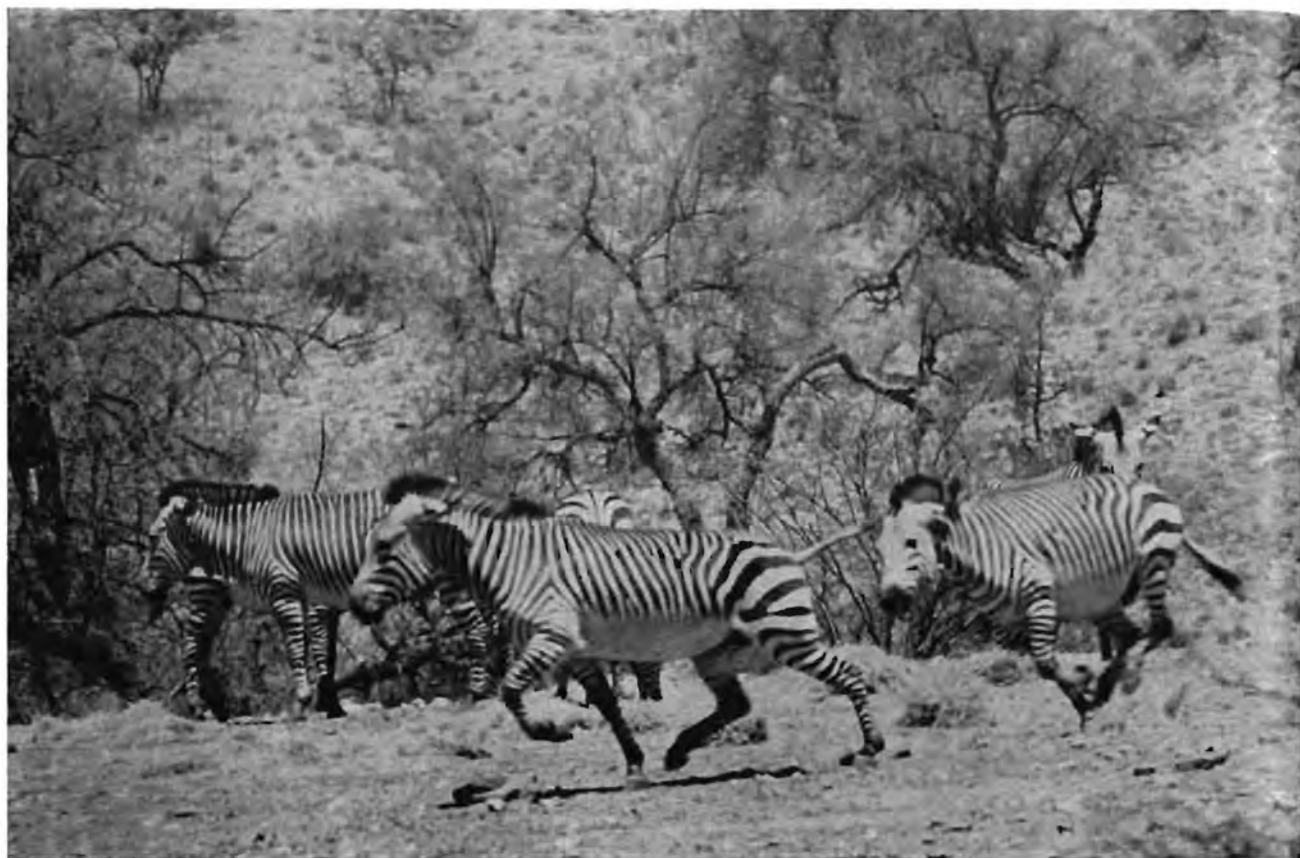


Plate 2: Two females engaged in "maintenance of hierarchy" activities. A higher ranking female chasing a lower ranking female. Photo E. Joubert.



Plate 3: Individuals awaiting their turn at a dust bowl where dust-bathing takes place in hierarchal order. Photo E. Joubert

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. This 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.

#### 4.5 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; Alec 1958; 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 than 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.

**4.6 Behaviour patterns between individuals****4.6.1 Individual recognition**

The success of the social hierarchy and even the maintenance of the Hartmann zebra social system depends 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 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.

**4.6.2 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 trampling 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 when 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 (See plate 2):

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 signal 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.

#### 4.6.3 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 Hart-

mann 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 females' 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.

#### 4.6.4 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.

##### 4.6.4.1 Between the female and her own progeny

The behaviour of the female towards her own young foal 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.

#### 4.6.4.2 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.

#### 4.6.4.3 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 author 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 shown 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.

Breeding unit 3.

Date:

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 ap-

proaches 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 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.

#### 4.7 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 mechanism 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.

##### 4.7.1 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.

#### 4.7.2 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 become 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.

#### 4.7.3 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.

#### 4.8 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 phases:

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

##### 4.8.1 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 be-

haviour 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 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.

##### 4.8.2 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 nasolateral 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 ritualized 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.

Breeding unit 5.

Date:

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.

#### 4.8.3 Copulation

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

#### 4.9 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 or 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 the 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 suckling, 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.  
Breeding unit 5.  
Date:  
26th November, 1969.

"9.30 a.m. 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 attempts 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 suckling behaviour. The releaser used by the foal to initiate this behaviour has already been discussed. Suckling 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

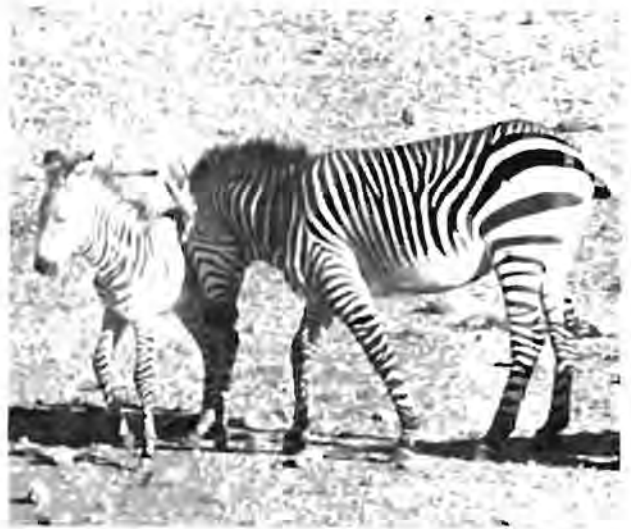


Plate 4: A typical behaviour pattern shown by female towards their foals — female rubbing her face against side of foal. Photo E. Joubert



Plate 5: A foal grooming its mother. Photo E. Joubert.



Plate 6: A foal laying its neck over that of the mother in an effort to initiate play. Photo E. Joubert.

suckled, 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 suckle 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 suckling took place however, was observed to decline fast, especially after the first two months. The newly-born foal suckles once every 50 to 70 minutes during daylight hours. At this stage suckling lasted approximately 50 to 75 seconds, followed by a period of five to 15 seconds during which the foal rested. Then it will suckle again for five to a maximum of 15 seconds. The regularity with which the foals suckle declines gradually to twice daily, at which time the female would start her "weaning of the foal" behaviour.

The number of times a foal suckles, as well as the duration of this suckling, 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 probably drawn out over a longer period than is 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 suckles 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.

#### 4.10 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 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.

##### 4.10.1 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 divided 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 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 guinea-fowl. 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 than 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.

#### 4.10.2 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, im-

mediately 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.

## V. THE DOMINANT MALE

### 5.1 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: