

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:

### 5.1.1 Herding behaviour

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

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

If the information above is analysed it shows the following: Male number one was removed from contact with the social organization of Hartmann zebra at a relatively early stage. He did not have the full benefit of learning whilst still with his original family group — neither did he have any training period with a group of bachelors. Despite this, when he reached sexual maturity he showed herding instincts. It appears as though the need for herding in this zebra male became so great that it was channelled into an outlet by herding springbok. This behaviour was also showed by adult male number two, which had had experience under natural conditions (he was caught while being with a breeding unit), and which also resorted to herding springbok. According to Lorenz (1963) a typical innate behaviour pattern shows characteristic accumulation properties with an increasing need to be performed the longer they are denied an outlet. This indicates:

- (i) that in the Hartmann zebra males, herding behaviour has evolved as an innate behaviour pattern.
- (ii) that the herding instinct exists and can find an outlet without having to be triggered by an oestrus female although this is normally the case.

### 5.1.2 The ability to face competition and to hold its own against other males

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

- (i) It suppresses actual lethal contests which endanger the survival of the individual, which is also the carrier of important genes.
- (ii) It functions as one of the mechanisms for holding the breeding unit together.
- (iii) It is also instrumental in setting up the breeding unit as an independent entity against other similar units.

### 5.2 The influence of the breeding unit on the dominant male

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

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

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

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

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

- (i) It appears as though the mere presence of a dominant male can inhibit any sexual behaviour by the bachelor males without any physical activity on his part directed at the bachelor males. On other occasions however, bachelor males did succeed in abducting young, in-oestrus females.
- (ii) Observations in the field showed that even on occasions when oestrus females were abducted by bachelor males, mating only took place after this herding activity (abducting) was carried out. Apparently herding activity, after being triggered by an oestrus female, is a prerequisite for mating in young sexually mature bachelor males.
- (iii) This behaviour by sexually mature bachelor males is indicative of a condition that has been

called by most ethologists "psychological castration". The influence of this "psychological castration" is only overcome by bachelor males when they actively engage in herding behaviour.

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

### 5.3 Behaviour towards other dominant males

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

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

That the ritualized challenge behaviour by a dominant male towards other dominant males also func-

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

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

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

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

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

#### 5.4 Challenge rituals

In the Hartmann zebra social organization challenge rituals only take place between dominant males. The functions of these highly ritualized activity patterns have already been discussed. Klingel (1967) does not describe any challenge rituals in the Burchell zebra. Although he mentions that fighting between males happens infrequently, it apparently does so with much greater regularity than in the Hartmann zebra, where it was observed only once during three years. Fighting behaviour in the Burchell zebra is not ritualized according to

Klingel, but owing to their comparatively harmless weapons no serious injuries are inflicted. The only behavioural trait found in dominant Burchell zebra males that may be compared with the challenge rituals in Hartmann zebra is called "Greeting behaviour" by Klingel (1967). Two of the three components in this behaviour, naso-nasal contact and naso-genital contact described by Klingel, is also found in the challenge ritual of the Hartmann zebra, but the "jump" with which this greeting ceremony is terminated is not present in the Hartmann zebra. Challenge rituals of various animal species have been described by a number of ethologists. The work by Estes (1968) on the wildebeest is, however, one of the most comprehensive. Many of the terms used by Estes to describe the various positions taken up by the participants, are self-explanatory. In the Hartmann zebra, antagonists take up a few similar positions and the applicable terms used by Estes can therefore be used to describe these positions in the Hartmann zebra's behaviour.

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

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

##### 5.4.1 The approach

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

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



Plate 7: The first step in the challenge ritual between two dominant males, the *Naso-nasal Contact*. Photo E. Joubert.



Plate 8: The *Reverse-Parallel Position* is usually the next step in the challenge ritual. Photo E. Joubert.



Plate 9: The *Naso-genital Contact* is also an important part of the challenge ritual. Photo E. Joubert.

#### 5.4.2 Engagement rituals

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

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

this position their horns are out of sight. In the Hartmann zebra this seems to be a more provocative position, as in Grant's gazelle (Walther, 1965), especially if the associated behaviour is considered. This takes the form of lifting the inner hind leg and feigning kicks backward, indicating willingness to engage in combat. At this stage the Hartmann zebra has two options: it may either indulge in *Naso-genital Contact* or the *Head/Rump Rubbing*. Normally however, the *Naso-genital Contact* precedes the *Head/Rump Rubbing*. Contrary to the wildebeest the dominant males do not show flehmen at this stage (it does occur when a dominant male confronts a bachelor unit). The *Naso-genital Contact* is of very short duration. The *Head/Rump Rubbing* is, however, normally of longer duration.

Tension is built up through the various foregoing rituals. This tension build-up is also indicated by the tail movements of the participants. In contrast with tail movements induced by insect disturbance, which is always rhythmic, even when the insect disturbance is high, tail movement owing to psychological tension is very erratic. The tail is also lashed from side to side rather than swept. One should also bear in mind that the whole ritualized challenge has evolved to reduce lethal fighting. Estes (1968) speculates on the significance of the

*Head/Rump Rubbing* behaviour, as it does not conform with the concept of the challenge rituals being a purely agonistic encounter. Comparing it with similar behaviour in other species he comes to the conclusion that it may be purely social grooming. This seems to be the case in the Hartmann zebra as well, where it functions to reduce the psychological pressure built up.

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

#### 5.4.3 Demonstration-threat marking

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

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

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

#### 5.4.4 Displacement activities

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

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

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

#### 5.4.5 Redirected activity

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

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

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

#### 5.4.6 Withdrawal

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

#### 5.5. Advertising dominance

With most territorial animals the advertising of ownership of a territory forms an important part of the day's activity pattern. This advertising may take the form of scent-marking territories or sometimes this advertising is vocal, as with birds. Wynne-Edwards (1962) called the morning and evening peaks of birdsong epideictic displays. Estes (1968) found that vocal displays are also used by wildebeest to some extent to warn off conspecifics. He noticed that this calling (grunts) by territorial wildebeest had no influence on females but did have a

definite intimidating effect on the passing males, but none on the territorial neighbours.

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

#### 5.6 Relations with bachelor units

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

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

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

It is furthermore noticeable that especially the older animals in the bachelor unit have prolonged spells of naso-nasal contact with the dominant male. In the naso-nasal contact the neck is stretched forward, the mouth is opened — without baring the teeth — and with a chewing motion the two animals sniff at each other's noses. It was observed that the Hartmann zebra have exceptionally long, thick



hairs scattered on their lips. It may be that this chewing motion is a form of tactile stimulus caused by the long hairs. The fact that it is especially noticed in situations where an attempt is made to avoid aggression between dominant and submissive animals (as between dominant male — submissive bachelor; female — foal; dominant male — female and dominant male — dominant male, but never between females of a breeding unit) makes one wonder whether it does not have a soothing effect on the participants. Klingel (1967) describes nasolabial contact amongst individuals of similar classifications in the Burchell zebra social system and also in the Hartmann zebra (1968).

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

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

### 5.7 Persistence in a breeding unit

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

In the study on the Hartmann zebra only those animals in the Daan Viljoen Game Reserve could be observed continuously over a period of three years. Frequent visits were made to the other study areas but the various family groups could only be observed for short periods. Although no figures

are available for the other study areas, the overall impression was that in the Hartmann zebra, the dominant male, as in Burchell zebra, shows a high degree of persistence in a breeding unit. This is also borne out by the known individuals at the Daan Viljoen Game Reserve. Over a period of three years the dominant male only changed twice in different breeding units. In one instance the dominant male was forced to abandon this group owing to old age, and in the other instance, the dominant male injured a leg and was eventually forced to abandon his breeding unit as he could not keep up with them.

## VI. THE BACHELOR UNIT

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

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

- (i) The mother of the foal has another foal and the relationship between mother and foal is broken.
- (ii) There are no other males of the same age in the breeding unit, which they then leave to go and look for playmates of their own age.
- (iii) A bachelor unit with young foals of similar age may be in the vicinity of the breeding unit, the young of which then leave to join the bachelor unit.

This may be true to some extent but in the Hartmann zebra it still leaves some questions unanswered. Only a third of the foals in any breeding unit leave the unit when the relationship between them and their mothers is broken. From this stage onwards they usually leave the breeding units of their own accord, sometimes more than two years later. One of the first male foals to be born in the Daan Viljoen Game Reserve when this project was started there in 1968 was 5BA. Approximately three months later another male foal 5DB was born.

The two became inseparable. They both left the breeding unit of their own accord when 5BA was two years old. They wandered around on their own for almost a week, sometimes in the vicinity of a bachelor unit, before they joined it. In this instance it was definitely not a case of looking for playmates of their own age — they had each other.

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

### 6.1 Age composition

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

The age composition of a bachelor unit is quite dynamic and shows a constant change as animals come and go. The youngest males might be only 14 months old, whereas the oldest might be quite senile. As can be seen in figure 2 a graph showing the age composition of bachelor units shows two peaks. The first peak starts at an age of 14 months and has a steep rise to the apex at approximately four years. From here the graph drops sharply again, virtually to the horizontal axis and stays so low until approximately 10 years. From here the graph shows another gentle rise with a second peak at approximately 12 years. The second peak does not reach the same height as the first peak, however, the reason for this being that the number of the adult males is considerably less, being reduced by predators, accidents, diseases or old age.

It was found that bachelor units consisted of any number of animals between one (invariably adult animals) and 15, the average size being approximately six. The latter, however, may consist of two or more bachelor units that have joined. Usually after a few days they split again into smaller units. It was found that units with only adult animals would on the average be smaller than units that also consisted of younger animals. Although bachelor units frequently consisted of only adult animals,

one never found bachelor units with only young animals. In the units with pre-dominantly young animals there would always be at least two adult males. In these latter units most of the young animals would have an age of between two and four years.

### 6.2 Internal organization

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

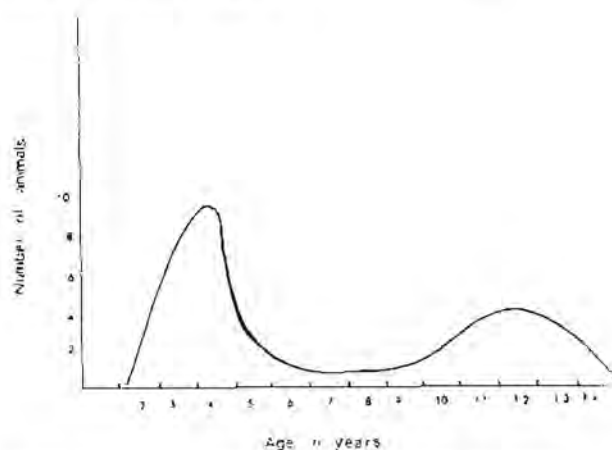


Figure 2. Age composition of bachelor units in *Equus zebra hartmannae*.



Plate 10: Two young males engaged in a "greeting game" which is a copy of the challenge rituals of dominant males. Photo E. Joubert.

### 6.2.1 Relations between bachelor males

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

#### 6.2.1.1 Playfighting

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

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

#### 6.2.1.2 Urination-flehmen sequence

Klingel (1967) mentions flehmen behaviour shown by young males in the Burchell zebra. They showed flehmen behaviour after smelling at fresh dung or a spot where another member of the bachelor group had urinated. They themselves then in turn defaecated or urinated on this spot. In the Hartmann zebra something almost similar was noticed. The bachelor unit showed this behaviour of defaecation in sequence on the same spot without showing flehmen behaviour. When one of them urinated however, they all showed flehmen behaviour and urinated in sequence. When a dominant male was present this behaviour was even more marked. The flehmen was always followed by extensive nasonasal contact by all the animals present, intermingled with a clamour of submissive calls, as though the bachelor males were trying their best to ensure the dominant male of their submissiveness. As already discussed, flehmen behaviour is shown by a great number of ungulate species and is almost exclusively associated with reproduction in most species. Estes (1968), however, observed it also in the challenge ritual in the wildebeest, and has the following explanation for this behaviour in the wildebeest: With the flehmen behaviour the con-

centration of androgens in the urine offers an index to a male's reproductive — hence territorial — status. He furthermore states that this behaviour during the challenge rituals would be a checking of territorial credentials.

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

### 6.2.2 Hierarchy

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

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

### 6.2.3 New recruits

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

## VII. FORMING OF NEW BREEDING UNITS

### 7.1 Influence of oestrus

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

- (i) when the female which comes into oestrus is a young female. Older females which have already become an inseparable part of the breeding unit through their long association with it do not facilitate abducting by young inexperienced males.
- (ii) when the number of females in the breeding unit has reached or is close to saturation point. If the breeding unit is still small, the dominant male's own herding instincts will still be so strong that a young inexperienced male would not stand a chance.
- (iii) when there is a bachelor unit in the vicinity with sexually mature males which have had the stimulating experience of competition with fellow males and have reached a high position in the hierarchy of the bachelor unit.

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

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

## 7.2 Behaviour of female(s) to an encroaching male

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

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

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

## 7.3 "Habituating" of new males

This is one of the methods by which existing breeding units are sometimes taken over by a new male. Estes (1968) also describes it as a method which wildebeest males employ in gaining a territory. Maler and Hamilton (1966: 62) discussed habituation and extinction of animal behaviour at some length. They define habituation as the waning of responsiveness to repetitions of a constant stimulus, thus leading to the eventual extinction of a conditioned response.

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

#### 7.4 Splitting of existing breeding units

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

#### 7.5 Stability of a new breeding unit

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

### VIII. GENERAL DAILY ACTIVITY PATTERN

Although the daily activity patterns shown by Hartmann zebra are discussed more fully elsewhere (Joubert, 1972), the general tendencies are briefly outlined here for the sake of completeness.

#### 8.1 Nutritional activities

##### 8.1.1 Grazing pattern

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

Even during the rest periods of the day hardly any time passed without some of the animals starting to nibble for a few minutes. The grazing activity intensified again from about 1500 hours and normally reached its highest intensity shortly before last light. During the rest of the day the grazing pattern was rather erratic with feeding activity taking place at a rather leisurely pace (Joubert, 1972).

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

Another very conspicuous behavioural trait is the

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

##### 8.1.2 Nutritional activities of foals

Foals start grazing within a few days after birth, although they remain dependent on their mothers until weaned. Figure 3 shows the daylight suckling pattern of Hartmann zebra foals. This shows clearly that although suckling occurs throughout the day, two peak periods exist. These are between 08.00 hours and 10.00 hours in the morning and then again from 14.00 hours onwards in the afternoon, which coincides with the major feeding periods of the breeding unit.

##### 8.1.3 Drinking

Where the Hartmann zebra are hunted they normally come down to water during the night, sometimes before 22.00 hours, but more likely during the early morning hours after 04.00 hours. In areas where they are protected or not disturbed, as at waterholes high in inaccessible mountains, they drink any time throughout the day. This behaviour was observed at the rainwater pans on the Naukluft Mountain plateau, and certain localities along the Kuiseb River, as well as in the Daan Viljoen Game Reserve. They may visit the water at any time during the daylight hours and again from 19.00 hours to approximately 22.00 hours. When water is available they may drink daily, sometimes even twice daily, viz., early morning and late afternoon. It is not certain how long they can remain without water during the hot dry conditions but during the rainy season they may go two or more days without drinking (See figure 4).

#### 8.2 Social activities

##### 8.2.1 Hierarchy

Activities between the females of a family group to affirm social status occur throughout the day. These activities, however, reach a low point during the two major grazing periods and become more marked again as grazing activities decrease. Figure 5 shows a period of high intensity activity from approximately 09.00 hours. The other figures (9 and 11) illustrating comfort movements viz. dust bathing and rubbing, also show increased intensity from about the same time. This increase is no doubt due to the competition for the best shade, rubbing posts and a better position in the dust bathing sequence.

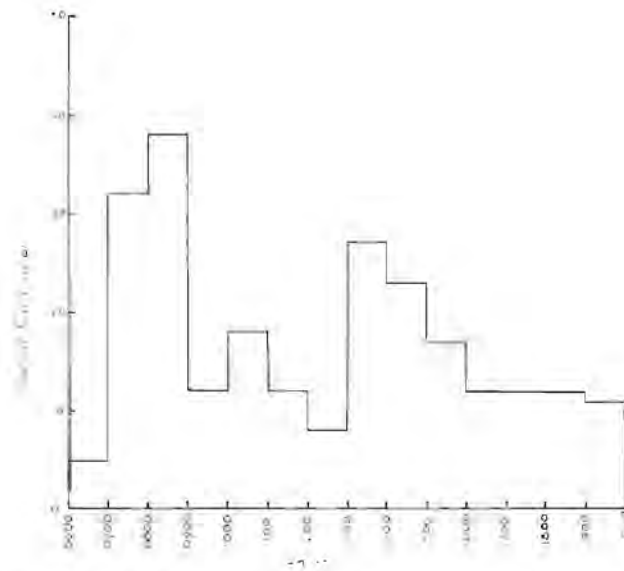


Figure 3: Daylight Suckling Pattern of Hartmann Zebra Foals.

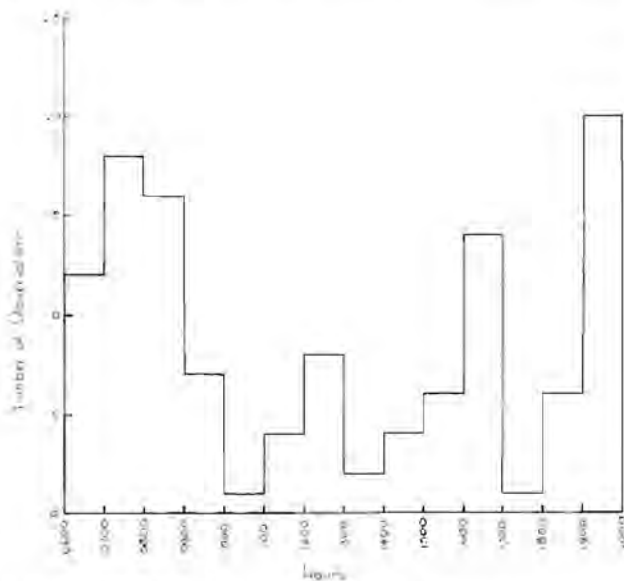


Figure 4: Daylight Drinking Pattern of Hartmann Zebra.

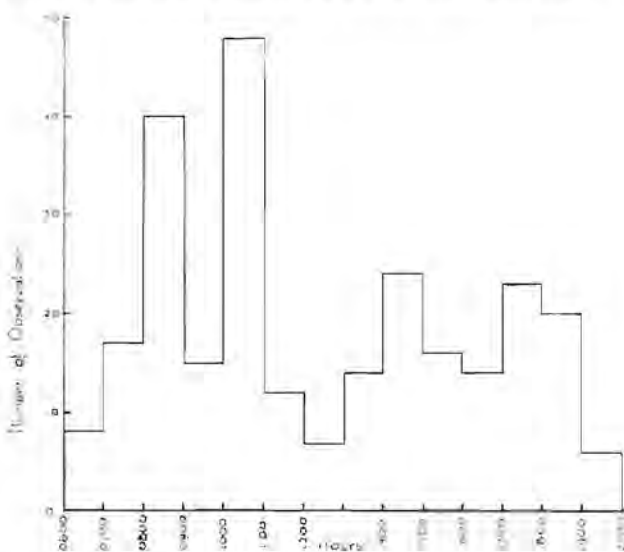


Figure 5: Hierarchical Activities of Hartmann Zebra Females.

### 8.2.2 Playing

This activity is indulged in mainly by the lone animal in a family group and the immature animal in the bachelor groups. In the former, play consists mostly of the running chasing variety while the latter becomes more serious and consists mainly of play-fighting. Play occur almost throughout the day as can be seen in figure 6 but with an higher intensity during the morning hours. This high intensity playing from 07.00 hours to 10.00 hours coincides with the major morning activity period.

### 8.2.3 Mating

Mating activity occurs throughout the day as shown by figure 7. Unlike most other activities, however, it shows a higher intensity during the afternoon from 15.00 hours.

### 8.2.4 Greeting rituals

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

## 8.3 Comfort activities

### 8.3.1 Resting

This is a very marked activity in the Hartmann zebra. A large percentage of the family groups under observation normally sought shelter in the shade. Usually, however, one or two individuals will stay out in the sun, either resting or grazing. Even during some of the relatively cooler winter months they would seek shelter in the shade of trees. As shown in figure 8 this happens from as early as 07.30 hours in the morning, thus shortly after first light. No animals were ever recorded standing in the shade later than approximately 17.50 hours. No clear correlation could be found between the time that most animals seek shelter in the shade and the peak of the temperature curve, apart from a small increase in this activity between 15.30 hours and 15.00 hours.

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

### 8.3.2 Dust-bathing

Hartmann zebras are compulsive dust-bathers. This activity is carried out with a very high frequency throughout the day and throughout the year. There is no clear indication of what the advantage of this is to the animal. It might be to reduce disturbance by insects. However, there is no decline in the rate at which this activity is performed during the winter.

ter months when the insects causing the disturbance are virtually absent. From figure 9 one may see that dust-bathing shows a clear pattern with peaks after the morning's grazing activity declines and then again before the afternoon's grazing activity reaches its peak. Insect irritation cannot be shown to have any clear peaks. However, there can be no doubt that insects are responsible for a certain amount of dust-bathing especially when the animals are resting in the immediate vicinity of dust bowls. It is possible that this dust-bathing, which also takes place on wet soil, is a "maintenance of the condition of the hide" activity.

Dust bowls are normally located at predictable places, usually on saddlebacks or ridges of mountains or in the bottom of the valleys that dissect the Khomas Hochland. They are usually situated in sandy or loamy soil and are approximately 2 to 2½ m across and anything up to 50 cm deep. Sometimes there are a few located close to one another. Newly graded roads are also used. To lie down, a zebra bends its forelimbs and stands on its knees. It then lowers the hindquarters to the ground. Getting up it gets onto its knees and then with a jerk pulls the hindquarters onto its feet. While lying down in the dust bowl it lies flat on its side, also resting the head on the ground. It then twitches the tail working dust in between the higher parts of the hindlegs. It will then roll onto its back and back to the original position — it never rolls completely over. Foal however, sometimes do. After doing this three or four times it will get up and then lie down on its other side. The whole performance is then repeated. Sometimes the animals will lie in this position in the dust bowl for several minutes before getting up.

8.3.3 Lying down

Adults were seldom seen to lie down except when taking a dust-bath. On the only two occasions that adult animals were observed to lie down the animals concerned were pregnant mares, heavy in foal. In both instances they did not lie down for longer than 25 minutes. Foals, however, lie down very often especially between 09.00 hours and 18.00 hours with peaks during 09.00 hours to 12.00 hours and 16.00 hours to 17.00 hours as illustrated by figure 10. The length of time spent lying down varies between 5 minutes and 55 minutes the average being 18.2 minutes (102 observations). An interesting aspect is that in all the abovementioned cases of lying down the foals did so in direct sunlight. On no occasion was one of them observed to seek the shelter of a tree to lie down in the shade. When lying down they did so flat on their sides with their heads also resting on the ground.

8.3.4 Rubbing

This nearly always takes place while the animals are resting in the shade of a tree or under overhanging rocks. Animals were very seldom seen to interrupt their grazing, just to rub themselves. The boles of trees were used to a very great extent in

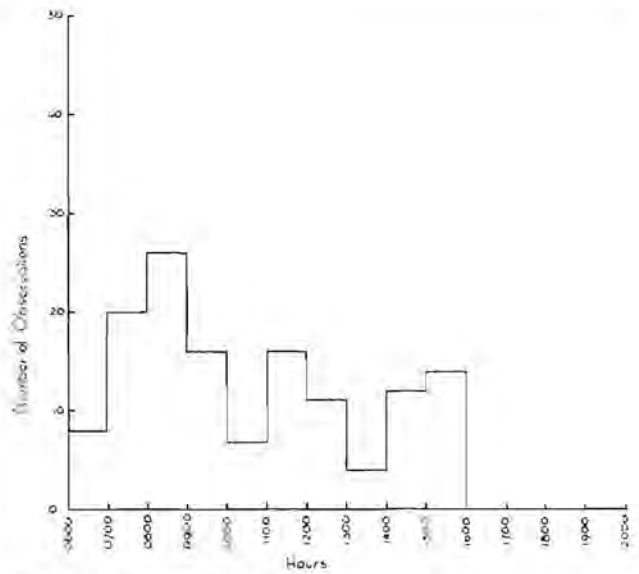


Figure 6: Playing Pattern of Hartmann Zebra Foals.

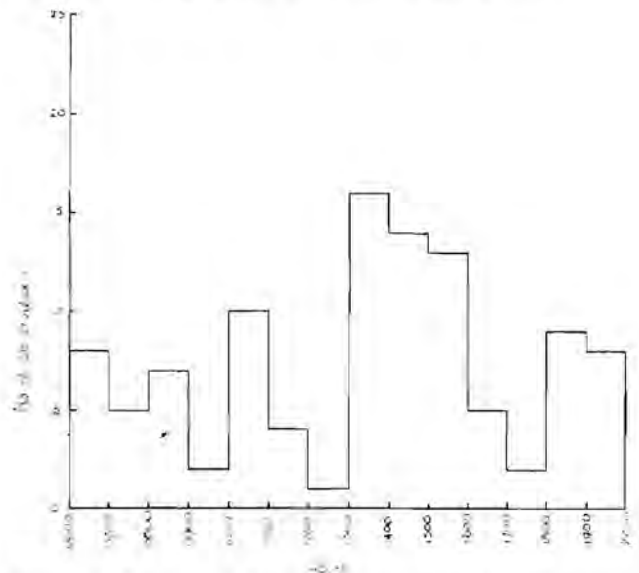


Figure 7: Pattern of Mating Behaviour in the Hartmann Zebra.

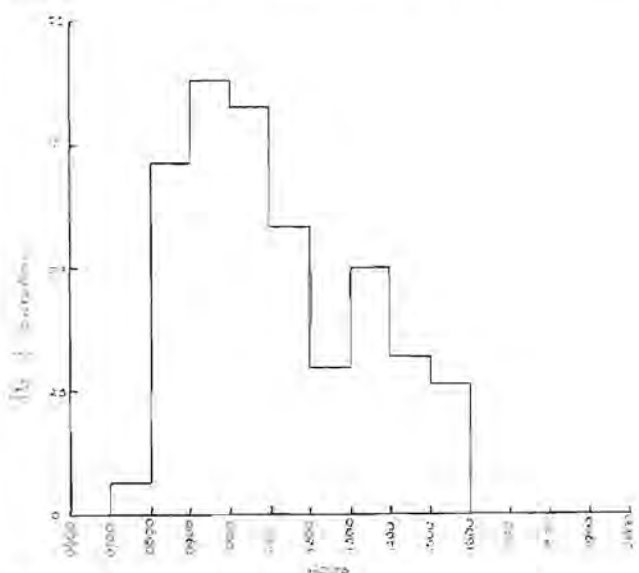


Figure 8: Resting in the Shade Pattern of Hartmann Zebra.

this activity although rocks were also utilized. The brunt of this rubbing activity was normally directed at the neck and the side of the body. If the bole grew at an angle or if a rock was used, the animal would try and straddle it to rub the insides of the hind legs and the rear part of the body. The face itself was very seldom attended to in comparison with the rest of the body. Only when a broken off

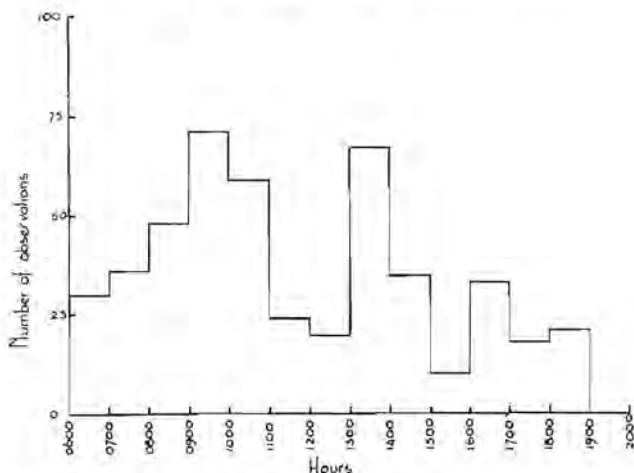


Figure 9: Dust-bathing Pattern of Hartmann Zebra.

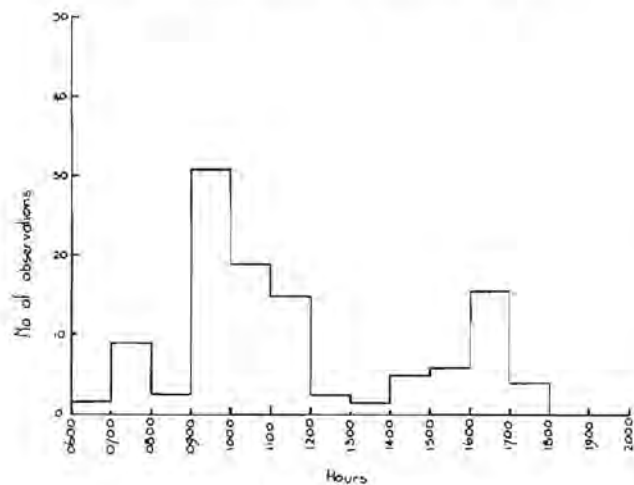


Figure 10: Lying down Pattern of Hartmann Zebra.

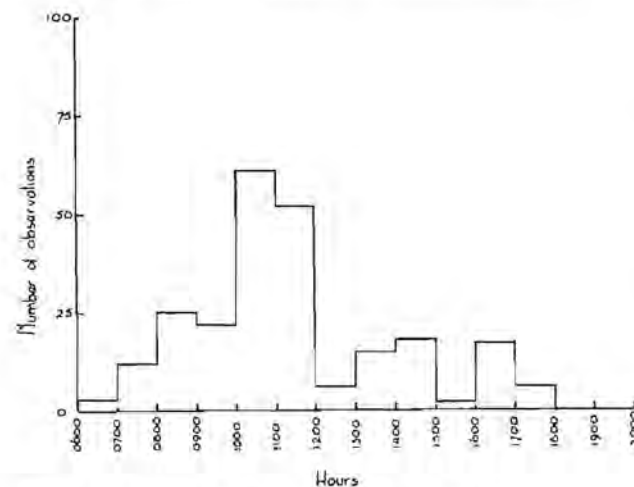


Figure 11: Rubbing Pattern of Hartmann Zebra.

branch was available would this be used for scratching around the eyes and ears and sometimes the neck. They often use their hind feet to scratch their heads (See figure 11).

### 8.3.5 Grooming

No grooming between adults of a breeding unit was ever noticed and only very seldom between mare and foal. Between foal and mare it occurs more regularly. This amicable behaviour by the foal no doubt serves to promote the maternal instinct in the female and also as a mechanism inhibiting aggressive behaviour in the female. When observed between mare and foal as well as between foal and mare it normally consisted of nibbling the neck and mane. No "licking" was ever seen such as is common with artiodactyls and certain carnivora (See figure 12).

## 8.4 Sanitary activities

### 8.4.1 Defaecation

In the field, animals defaecated between three and eight times a day. Figure 13 shows clearly that although defaecation can take place at any time during the day, this activity reaches a peak during the morning high intensity grazing period. It was noticed sometimes that when one animal in a zebra group defaecated it acted as an expression movement and nearly all the other animals would then follow suit.

### 8.4.2 Urination

Urination does not take place simultaneously with defaecation although it can precede or follow it with only a short interval in between. According to figure 14 an animal urinates throughout the day, normally between five to thirteen times a day during daylight hours.

## 8.5 Other activities

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

### 8.5.1 Walking

The major activity here consists of walking while not actively grazing. This takes place throughout the day. From figure 15 it may be seen that this activity starts in the morning with a high incidence. It then declines gradually; and it suddenly intensifies again to a high peak during the period 15.00 to 16.00 hours. Most of the other activities discussed elsewhere have a very low intensity during this time interval with the exception of grazing activity which shows a tendency to increase.

Klingel (1967) found that Burchell zebra have a specific sleeping place to which they retire every evening. In the morning they leave this sleeping



place and walk to the grazing area, sometimes as far as 15 kilometres away. No such behaviour was ever noticed in the Hartmann zebra. They would spend their nights anywhere in the Game Reserve and start feeding at that particular place in the morning. The daily distance covered by the Hartmann zebra varies considerably and depends on such factors as condition of the grazing and season of the year. On the average they cover approximately one to three kilometres per day while grazing and, at the most, five kilometres going to water. Even at the Naukluft Mountain Zebra Park and in the Khomas Hochland they are remarkably sedentary.

8.5.2 Running

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

IX. HOME RANGE

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

This annual movement (migration) of the Hartmann zebra is especially noticeable in the Oljovasandu and Kaokoveld areas where their movements are not yet restricted. They move down onto the pre-Namib flats when the first summer rains fall in this area. They stay here till the onset of the first cold weather when they move back into the protection offered by the mountainous transition belt forming the escarpment here. Even where their

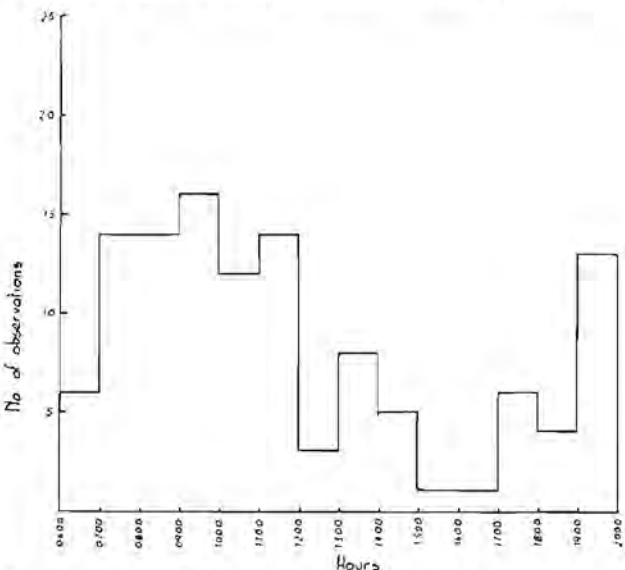


Figure 12: Grooming Pattern of Hartmann Zebra.

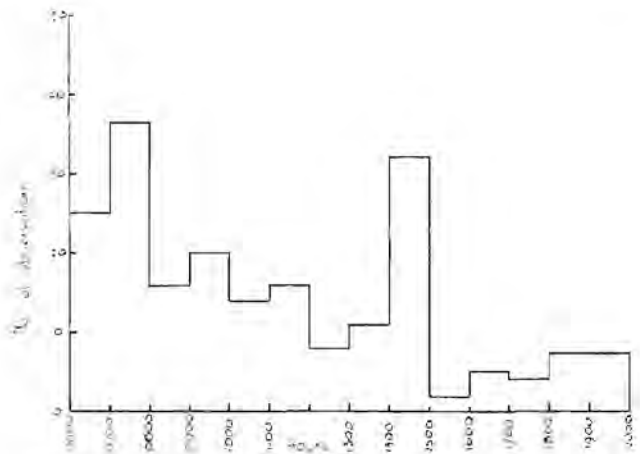


Figure 13: Defaecation Pattern of Hartmann Zebra

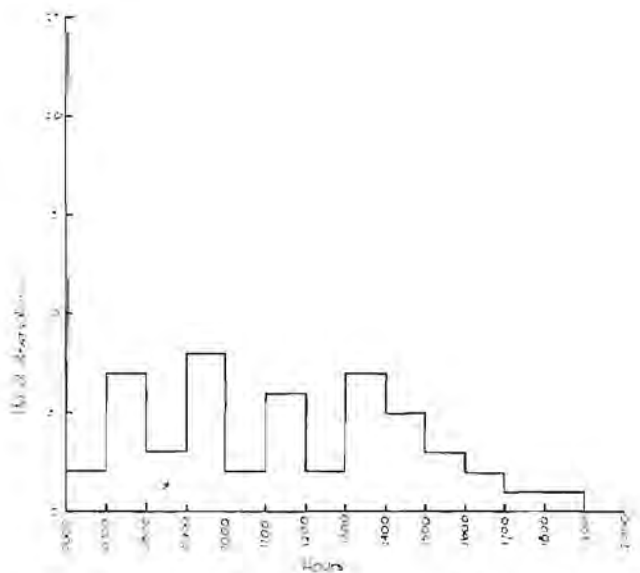


Figure 14: Urination Pattern of Hartmann Zebra.

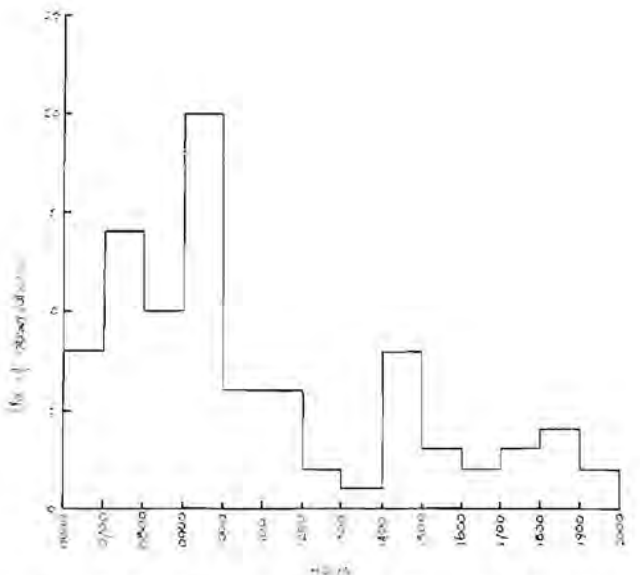


Figure 15: Walking without Grazing Pattern of Hartmann Zebra.

movements are restricted Hartmann zebra show this tendency to differentiate in summer and winter grazing areas. The northern part of the Naukluft mountains consists of a gentle undulating plateau, with several depressions which form large seasonal pans during the rainy season. During the rainy season and for the few months afterwards while these pans contain water the Hartmann zebra population of the Naukluft mountains concentrate in this area. As the water dries up they disperse over the rest of the mountain range to perennial waterholes and climatically protected areas.

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

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

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

Although these movements are primarily climatically orientated, as has already been discussed, they serve a useful purpose. The Hartmann zebra distribution lies for a thousand miles along the Namib desert in a very marginal area. With the low, erratic rainfall, the vegetative cover, especially

the grass, is extremely sensitive to overgrazing. Through their migration movements they thus practice rotational grazing, giving certain areas a rest period and a chance to recover. It also serves to ameliorate some of the temperature fluctuations that are so characteristic of this mountainous region along the desert. This differentiation between summer and winter grazing areas shows a remarkable adaptation by the Hartmann zebra to their environment. Even their social system may basically be an adaptation to their environment to establish a relationship of survival for the species as such.

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

## X. INTERSPECIFIC RELATIONS

### 10.1 With Burchell zebra

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

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

### 10.2 Other mammals

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

Although the threshold for the intention movement of running is very low if other zebra units should start running, other species running nearby seldom cause Hartmann zebra to stampede. Once

a herd of approximately 60 gemsbok appeared over a ridge running flat out past a breeding unit under observation. The zebra just watched them galloping past without attempting in the least to join the stampede.

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

### 10.5 Birds

The red-billed oxpeckers *Buphagus erythrorhynchus*, do not occur in the distribution area of the Hartmann zebra but two other bird species, the drongo *Dicrurus adsimilis adsimilis* and the pale-wing starling *Onychognathus nabouroup nabouroup*, seem to fulfil the oxpecker's functions in these regions. Actually there seems to be a bit of competition at times as it has been observed that a drongo would chase pale-wing starlings away from a zebra.

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

## XI. ABSTRACT

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

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

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

The principles of behaviour shown by the dominant male are discussed at great length. It is shown that the herding behaviour of males is an innate activity pattern. This innate herding drive by the dominant male is in an inverted ratio to the number of females in the breeding unit. The relationship between dominant males of various breeding units bears a certain resemblance to a territorial social system. A periphery effect is obtained when two breeding units come close enough to trigger the challenge rituals between the dominant males. The challenge ritual is analysed.

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

The home range of these animals as well as their interspecific relations are discussed.

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