

SOCIAL ORGANISATION OF THE CAPE  
MOUNTAIN ZEBRA *EQUUS Z. ZEBRA* IN THE  
MOUNTAIN ZEBRA NATIONAL PARK\*

B. L. PENZHORN  
*c/o 180 Anderson Street*  
*Brooklyn*  
*Pretoria*  
*0181*

*Abstract* — The social structure of Cape mountain zebras consists of breeding herds of one stallion, one to five mares and their offspring, as well as bachelor groups. Breeding herds remain stable over many years and when the stallion is displaced by another, the mares remain together. A dominance hierarchy exists, but leadership is random. Foals leave their maternal herds at a mean age of 22,3 months. The herd stallion tries to prevent the foals from leaving the herd. Bachelor groups are not as well defined as breeding herds, but core groups could be identified through a principal components analysis ordination. Family ties may be important in the establishment of core groups. Bachelors succeed in becoming herd stallions when about five years old. Aspects of the possible evolution of the social structure are discussed.

*Introduction*

The Cape mountain zebra *Equus z. zebra* Linn. 1758 is one of the rarest mammals in the Republic of South Africa and in the world. The total population does not exceed 200 individuals. Of these, about 75% are concentrated in the Mountain Zebra National Park (MZNP). This Park is one of the so-called “species reserves” administered by the National Parks Board of Trustees. The prime objective in the management of the MZNP is to ensure maximum reproductive success of the Cape mountain zebra population. It was proclaimed in an effort to preserve a subspecies from extinction and not primarily as a sample of an ecosystem. Although the Cape mountain zebra in the Park were breeding and increasing, albeit slowly, virtually nothing was as yet known about the population. The present study was therefore initiated to identify, if possible, limiting factors in the ecology of the Cape mountain zebra in the MZNP with a view to re-

---

\*Part of a D.Sc. (Wildlife Management) dissertation submitted to the Faculty of Science, University of Pretoria.

moving any such obstacles which could prevent maximum reproductive success by the zebras.

In addition to the social organisation, the behaviour, habitat preference and population attributes were also investigated. The study was commenced in May 1971 and intensive observations were continued until October 1973. The Park was visited regularly thereafter until January 1976, when the study was terminated.

### *The study area*

The study was conducted in the MZNP which by road is situated 24 km west of the town of Cradock in the Cradock Division, Province of the Cape of Good Hope, Republic of South Africa.

Area: 6 536 ha.

Geographical coordinates: 32°15'S, 25°41'E.

### *Topography*

The Bankberg is situated southwest of Cradock in the Cape Midlands. The MZNP covers an amphitheatre on the north-facing slopes of the Bankberg, mainly the catchment of the Wilgerboom River (Fig. 1). The southern boundary of the MZNP follows the summit of the Bankberg at an elevation of *ca* 1800 m or more above sea level. Spitskop, the highest point in the Park and in the vicinity of Cradock reaches 1 957 metres. The northern slopes of Bankberg form a series of steep-sided kloofs (Grootkloof, Fonteinkloof, etc.) where the Wilgerboom River and its tributaries originate. The Wilgerboom River runs in a north-north-easterly direction, bisecting the Park and joining the Great Fish River north of Cradock. The westernmost parts of the MZNP fall in the upper catchment area of the Kareebosch River, another tributary of the Great Fish. A series of dams has been built in the Wilgerboom River in the Park, ensuring a permanent flow in the river, except during severe droughts.

The high ridge running parallel to the western boundary from Kranskop (1 800 m) in the southwest serves as a watershed between the catchments of the Wilgerboom and Kareebosch Rivers. Two east-facing kloofs adjoin this ridge near the northern boundary of the MZNP, before it develops into an extensive plateau known as Rooiplaat, at an elevation of 1 300 m to 1 400 metres. The eastward extension of the ridge north of the northernmost kloof (Boesmankloof) is known as Babylons Toren.

Where the Wilgerboom River leaves the Park at its northern boundary, the elevation is about 1 200 m. Two small, isolated plains occur in the valley of the Wilgerboom River: Springbokvlakte; near the northern boundary, at an elevation of 1 200m—1 250 m and the other near the Berghof and Weltevrede homesteads at 1 300 m—1 350 metres.

*Geology*

The geological formations in the MZNP represent sandstone, siltstone and mudstone of the Lower Stage, Beaufort Series, Karoo System, and post-Karoo dolerite intrusions (Toerien 1972).

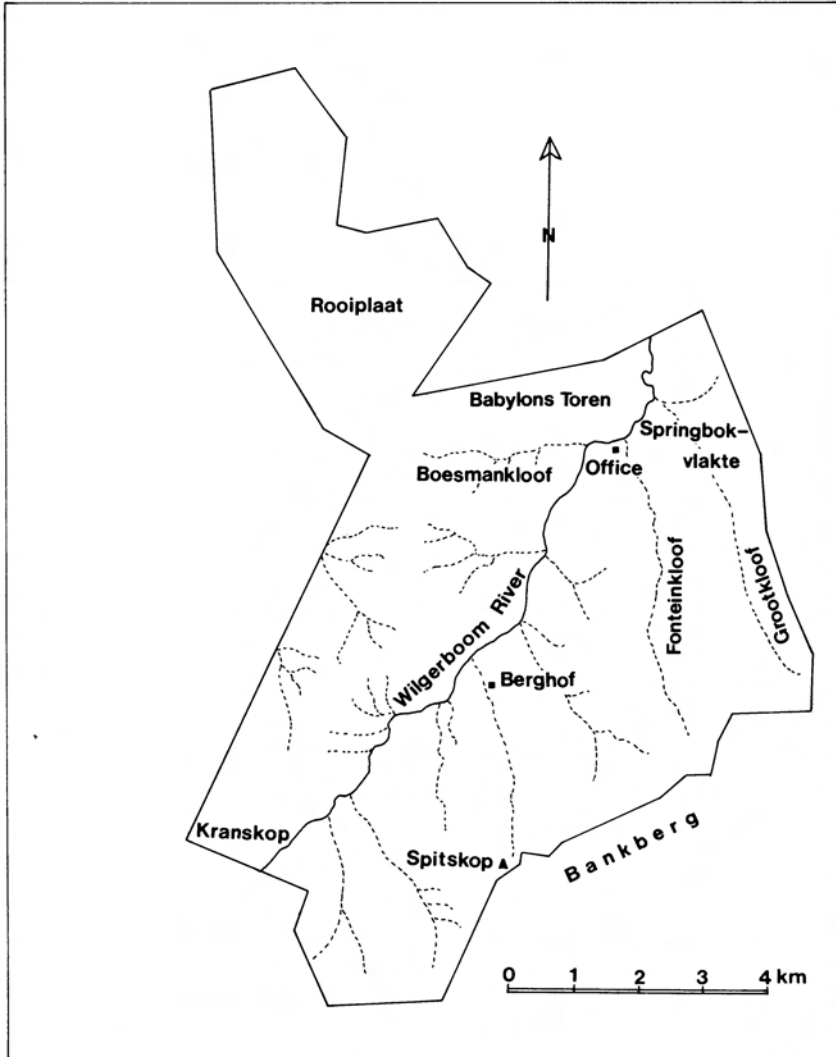


Fig. 1. Map of the Mountain Zebra National Park, Cradock Division, Cape Province, Republic of South Africa.

## Vegetation

The vegetation of the Bankberg and higher reaches of the MZNP is Karroid *Merxmuellera* Mountain Veld (Acocks 1975). The dominant grass is *Merxmuellera disticha* and although it may be the natural dominant in the rocky sandstone parts, Acocks suggested that *Themeda triandra* and *Tetrachne dregei* may be the natural dominants in all doleritic parts and all parts covered with soil. Further grasses are *Ehrharta calycina*, *Eragrostis chlorome-las*, *Melica decumbens*, *Eustachys paspaloides* and *Festuca scabra*. A rich variety of forbs and dwarf shrubs occurs, e.g. *Diascia capsularis*, *Pelargonium ramosis-simum*, *Stachys aethiopica*, *Sutera* spp., and *Othonna* species.

The northernmost parts of the MZNP fall in the False Karroid Broken Veld. Acocks stated that in this area this veld type is probably the result of the spread of elements of the open, grassy Karroid Veld of the mountains and of invasion by Central Lower Karoo into grassveld of dry *Cymbopogon-Themeda*-veld type, accompanied by overgrazing and eroding of the grass-veld. Typical dwarf shrubs of the Karoo vegetation are common in this area and *Becium burchellianum* is a distinctive species. The two main veld types are separated by Karroid *Merxmuellera* Mountain Veld replaced by Karoo (Acocks 1975).

Along the watercourses in the valley and in the kloofs, dense stands of *Acacia karroo* up to 8 m tall develop. Other species in this area include *Maytenus heterophylla*, *Diospyros lyciodes*, *Rhus* spp., *Lycium* spp. and *Clematis brachiata*. *Acacia karroo* has also spread to the hillsides. On rocky outcrops the following tree species occur: *Celtis africana*, *Olea africana*, *Cussonia paniculata*, *Rhus* spp., and *Dodonaea viscosa*. The Rooiplaat plateau is virtually treeless, but a few *A. karroo* trees occur in sheltered areas. The northern side of Babylons Toren has a fairly dense cover of *A. karroo*.

A check-list of the flowering plants recorded in the Park has been compiled (Penzhorn 1970, 1977a).

## Climate

### Precipitation

The monthly precipitation recorded in the MZNP during the 12-year period July 1962—June 1974 is given in Table 1. During this period 70,9% of the total precipitation was recorded between October and March and 29,1% during April to September. The annual precipitation was therefore calculated per wet season from July to June, rather than for a calendar year. The three-month period with the highest total precipitation was January to March, when 47,4% of the total precipitation was recorded. March had the highest mean precipitation (82,6 mm) and September the lowest (7,7 mm). During six years, no precipitation was recorded in July, during five years none in June, during four years none in August and Sep-

Table 1

*Precipitation (in mm) recorded in the Mountain Zebra National Park during the 12-year period July 1962 to June 1974*

MONTH	PRECIPITATION												Mean
	62/63	63/64	64/65	65/66	66/67	67/68	68/69	69/70	70/71	71/72	72/73	73/74	
July	0,0	43,7	0,0	35,6	0,0	9,0	0,0	0,0	0,0	45,0	3,5	1,0	11,5
August	4,6	6,1	26,4	0,0	0,0	4,0	13,0	0,0	58,0	87,0	0,0	21,0	18,3
September	0,0	8,1	10,7	0,0	10,0	0,0	35,0	7,0	0,0	14,0	7,0	0,5	7,7
October	6,3	45,0	27,2	62,0	3,0	23,0	22,0	54,2	16,5	30,0	25,0	28,5	28,6
November	56,1	80,3	24,6	69,3	2,0	25,0	13,0	24,0	17,0	57,5	0,0	11,0	31,7
December	7,6	40,6	15,5	0,0	20,5	6,0	51,0	10,5	101,0	18,0	0,0	35,5	25,5
January	112,0	23,9	32,8	20,6	55,0	54,0	18,0	24,5	106,0	44,5	26,5	87,0	50,4
February	23,1	29,2	35,1	27,9	37,0	36,0	6,0	32,5	59,0	59,5	58,5	72,0	39,7
March	129,3	52,8	20,6	30,5	95,0	93,0	75,0	2,5	77,0	84,0	123,0	208,0	82,6
April	66,3	8,4	59,4	10,0	49,0	46,0	67,1	17,5	30,0	51,0	43,5	15,0	38,6
May	8,4	6,4	1,8	29,0	59,0	13,0	18,0	28,0	18,5	16,5	15,5	13,0	18,9
June	7,1	52,3	20,3	0,0	16,0	0,0	0,0	0,0	2,5	15,0	0,0	18,0	10,9
Total	420,8	396,8	274,4	284,9	346,5	309,0	318,8	200,7	485,5	522,0	302,5	510,5	364,3

tember, during two years none in December and once none in November. The longest period without precipitation was three months (June—August 1969). Most of the precipitation occurred in the form of rain, but a few snowfalls (up to 20 cm) were recorded each winter. Hail occurred infrequently.

*Temperature and relative humidity*

The ambient temperature and relative humidity were recorded on a thermohygrograph in a Stevenson Screen located near the Warden's office in the Wilgerboom River Valley. The results of the recordings in 1969, 1971 and 1972 are given in Table 2.

Table 2

*Average air temperature and relative humidity recorded in the Mountain Zebra National Park during 1969, 1971 and 1972*

MONTH	TEMPERATURE (°C)				RELATIVE HUMIDITY (PERCENT)			
	Maximum		Minimum		Maximum		Minimum	
	<i>Mean</i>	<i>Range</i>	<i>Mean</i>	<i>Range</i>	<i>Mean</i>	<i>Range</i>	<i>Mean</i>	<i>Range</i>
January	29,1	18 to 37	13,7	7 to 21	72,5	46 to 96	25,0	14 to 50
February	27,4	15 to 37	12,6	7 to 21	83,4	52 to 95	31,3	14 to 72
March	24,9	13 to 34	11,6	5 to 18	58,9	47 to 94	39,9	13 to 68
April	19,3	6 to 28	6,4	1 to 13	86,5	73 to 95	34,4	16 to 71
May	16,8	8 to 25	3,9	-5 to 13	85,3	58 to 96	35,1	14 to 66
June	15,0	7 to 23	0,4	-7 to 10	83,2	36 to 96	33,7	18 to 57
July	15,8	5 to 22	-0,1	-6 to 8	76,1	42 to 96	29,8	15 to 61
August	17,6	3 to 28	1,0	-7 to 8	69,5	28 to 96	27,8	12 to 80
September	19,4	6 to 32	4,1	-6 to 18	65,2	19 to 94	28,4	11 to 87
October	22,8	9 to 35	7,7	-1 to 15	73,1	20 to 97	31,4	14 to 92
November	25,4	12 to 36	9,5	1 to 17	74,2	17 to 94	28,0	14 to 69
December	28,2	17 to 36	11,5	4 to 12	75,3	33 to 97	26,6	11 to 46

The mean maximum temperatures varied between 29,1°C in January and 15,0°C in June and the mean minimum temperatures between 13,7°C in January and -0,1°C in June. There were marked differences between daily maximum and minimum temperatures and also wide ranges within these. The highest maximum temperature (37°C) was recorded in January and February and the lowest minimum temperature (-7°C) in June. During October to March the maximum temperature exceeded 20°C. Mini-

imum temperatures below 0°C were recorded from May—October. In October 1971 this occurred twice during cold spells when -1°C was recorded. During both other years, temperatures in October never dropped below 0°C.

The monthly maximum humidity varied between 58,9% and 85,3% and the mean minimum between 25,0% and 34,9 percent. No pattern was readily discernible.

In order to investigate possible seasonal differences in behaviour of the Cape mountain zebra, two seasons were defined, *i.e.*:

summer: the six-month period from October—March, when the mean maximum temperature exceeds 20°C and *ca* 70% of the annual precipitation occurs.

winter: the six-month period from April—September, when the mean maximum temperature is below 20°C and only *ca* 30% of the annual precipitation occurs.

### *Wildlife*

In addition to the Cape mountain zebra, the only large mammals occurring in the MZNP at its inception were mountain reedbuck *Redunca fulvurufula*, grey rhebuck *Pelea capreolus*, grey duiker *Sylvicapra grimmia*, steenbok *Raphicerus campestris* and klipspringer *Oreotragus oreotragus*. The following antelope were subsequently re-introduced (or introduced) (Penzhorn 1971): eland *Taurotragus oryx*, black wildebeest *Connochaetes gnou*, red hartebeest *Alcelaphus buselaphus caama*, blesbok *Damaliscus dorcas phillipsi*, springbok *Antidorcas marsupialis*, gemsbok *Oryx gazella* and reedbuck *Redunca arundinum*. Gemsbok may have occurred in the northern parts of the Cradock Division (Skead 1958), but reedbuck are definitely extralimital (Ansell 1971). The reedbuck have not established themselves.

At a census in November 1973, antelope numbers were as follows:

mountain reedbuck	<i>ca</i> 1 000
springbok	<i>ca</i> 660
blesbok	<i>ca</i> 250
black wildebeest	167
eland	106
gemsbok	38
red hartebeest	36
grey rhebuck	7
reedbuck	1

At various times in the past it has become necessary to reduce the numbers of some of these antelope and springbok, blesbok, black wildebeest and eland have been captured for translocation elsewhere. The springbok, especially, are extremely prolific breeders and their numbers are reduced annually, usually by cropping (Penzhorn 1974).

The MZNP contains no large carnivores. De Graaff and Nel (1970) and Nel and Pretorius (1971) listed 33 small mammal species recorded in the Park. A total of 172 bird species has been recorded in the MZNP (Skead 1965; Penzhorn & Bronkhorst 1976; Penzhorn 1977b), of which only the ostrich *Struthio camelus* was re-introduced. No systematic collecting of reptiles or amphibians has been undertaken.

## Methods

### Identification

The stripe pattern of a zebra is a characteristic of the individual and no two are exactly alike. This was used by Klingel (1967) in the identification of 600 Burchell's zebra *E. burchelli* individuals of the total population of 5 500 in the Ngorongoro Crater, Tanzania. Joubert (1972) could identify the 48 Hartmann zebras *E. z. hartmannae* in the Daan Viljoen Game Reserve, South West Africa, by the same method. It was also used with great success during the present study.

The two sides of a zebra are not mirror images and a photograph of each side was pasted onto a 10cm x 15cm card with the relevant information concerning each individual written on the card, e.g. date or year of birth (if known), mother, date of leaving maternal herd, etc. (Fig. 2). An Asahi Pentax Spotmatic Motordrive camera and a 500 mm Takumar lens were used for the photographs.

By December 1971 all the individuals in the MZNP had been recorded,



Fig. 2. A card used for individual identification of Cape mountain zebras.



as no new individuals other than new-born foals were seen after this date. Although most individuals were eventually recognised on sight, the cards were taken along to each observation session, as it was often handy to check on an individual's birth date or relationships.

Numbers were assigned to individuals on the following basis:

The bachelors encountered at the start of the study were all numbered "A" with an additional numeral, *i.e.* A<sub>1</sub>, A<sub>2</sub>, A<sub>3</sub>, *et cetera*. The letters from B onward were assigned to the breeding herds. The numeral "1" was always assigned to the herd stallion, therefore B<sub>1</sub>, C<sub>1</sub>, D<sub>1</sub> etc. were herd stallions. The mares in each breeding herd were numbered from "2" onwards, *i.e.* B<sub>2</sub>, B<sub>3</sub>, B<sub>4</sub>; C<sub>2</sub>, C<sub>3</sub>, C<sub>4</sub> *et cetera*. The foals in each breeding herd were awarded numbers following on that of the last mare. If, for instance, breeding herd B contained three mares, the last mare would be B<sub>4</sub>. The foals were therefore numbered B<sub>5</sub>, B<sub>6</sub>, B<sub>7</sub> *et cetera*. Subsequent foals were added, thus the foals of mare C<sub>2</sub> were numbered C<sub>8</sub>, C<sub>12</sub> and C<sub>17</sub>. This method worked well, as there were fewer breeding herds than letters of the alphabet. However, the system used by Joubert (1972) would be more practical in large populations. Joubert numbered the herds and assigned letters to the individuals, e.g. 2A would be a herd stallion, 2B a mare, 2BA her first foal, 2BB her second foal, *et cetera*.

The MZNP population was small enough for the identification system to be handled easily and a systematic identification and reference system for zebras as proposed by Petersen (1972) was not necessary. Such a system would be important in the study of large populations.

The advantages of using individual characteristics for identification are obvious. The animals need not be marked and therefore the disturbance of capturing and marking large numbers of individuals is obviated. Capturing large numbers of animals incurs a lot of time and expense. Furthermore, all the individuals in the population can be identified, whereas with marking this is seldom, if ever, the case.

Doctor H. Klingel\* visited the MZNP in 1965 and 1967 and photographed most of the individuals. This information was generously made available by Klingel at the initiation of the present study and contributed immensely to the study. The fact that the ages of 117 individuals were known at the termination of the study (all individuals less than 11 years old) is largely due to the initial investigations by Klingel. Some individuals could be recognised from dated photographs taken by the official photographers of the National Parks Board of Trustees. Mr. A. Bannister, Johannesburg, kindly made available photographs taken in 1969 and 1970, enabling the exact birth date and relationships of some individuals to be identified.

---

\*Zoologisches Institut der Technischen Universität, Braunschweig, Germany (BRD).

## *Observation*

Observations were usually made with a pair of Leitz Trinovid 10x40 binoculars. Most observations were made from a vehicle, as this enabled a close approach to the animals observed. While the presence of a vehicle was tolerated by the zebras, the appearance of a human invariably caused alarm and often resulted in flight.

In dawn to dusk observations, the first breeding herd encountered was observed during that day. In a few cases where the herd under observation moved into inaccessible terrain and could no longer be observed, the first subsequently encountered herd was observed for the remainder of the day. During summer these observation periods occasionally lasted from shortly after 05h00—19h30.

Night observations were attempted, but without success. Observations with spotlights were not representative of normal activities, as the zebras reacted to the lights. Observations during nights of fullmoon proved feasible, although individuals could not be recognised. As soon as the animals moved out of sight, however, the headlights of the vehicle had to be switched on in order to negotiate the rocky terrain in following the animals. This invariably caused panic in the zebras. The attempts at night observations therefore had to be abandoned.

## *Social Organisation*

The social organisation of mountain zebras was described by Klingel (1968) and Joubert (1972) as basically consisting of discrete breeding herds and bachelor groups. Klingel used the terms "family" and "family group" to describe the association of a stallion and mares. Joubert pointed out that this may be misleading as these terms are more applicable to a stallion and a mare with their offspring rather than to a stallion and a number of mares, which are probably unrelated, and their foals. Joubert therefore introduced the term "breeding unit" which is used here, except "herd" being used in preference to "unit".

### *Breeding herds*

#### *Structure*

In the Cape mountain zebra population in the MZNP each breeding herd consists of a single adult stallion, one to five mares and their offspring. The size of a breeding herd varies according to the number of foals born to the herd and older foals leaving their maternal herds.

When the present study was initiated in June 1971, one breeding herd comprised five adult mares, the maximum number of mares recorded.

During January—March 1972 this herd comprised seven foals in addition to the stallion and five mares, with a total of 13 individuals, the maximum recorded. The herd split up in October 1972.

On 30 June 1973 the MZNP population consisted of 129 individuals, of which 98 (76%) were grouped into 21 breeding herds with a mean of 4.7 animals per herd (range 2—8) (Fig. 3). The breeding herds contained a mean of 2.4 mares per herd (range 1—4) (Fig. 4). With the growth of the

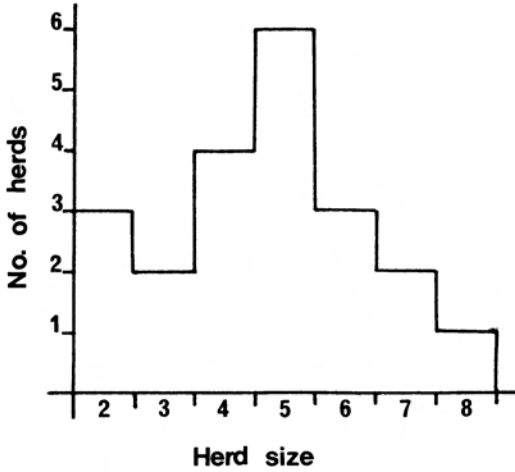


Fig. 3. Frequency distribution of herd size of 21 Cape mountain zebra breeding herds in the Mountain Zebra National Park as at 30 June 1973.

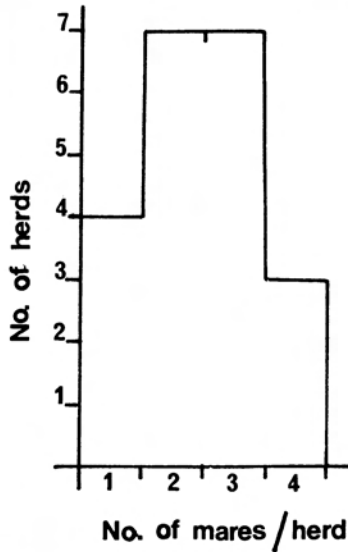


Fig. 4. Number of adult Cape mountain zebra mares per herd in 21 breeding herds in the Mountain Zebra National Park as at 30 June 1973.

population from 59 in 1965 to 145 in 1974, the mean herd size and mean number of mares per herd have declined (Table 3) and are at present vir-

Table 3

*Herd size and number of mares per breeding herd in Equus z. zebra and E.z. hartmannae in southern Africa*

Subspecies	Year	HERD SIZE			NO. OF MARES	
		n	mean	range	mean	range
<i>E.z. zebra</i>	1965*	9	5,5	2-8	2,8	1-4
	1973**	21	4,7	2-8	2,4	1-4
<i>E.z. hartmannae</i>	1965*	82	4,7	2-8	2,2	1-4
	1971***	52	no data		2,26	no data

\*Klingel (1968)

\*\*Present study

\*\*\*Joubert (1972)

tually identical to that of Hartmann zebras (Joubert 1972), but for a slightly higher mean number of mares per breeding herd. In Burchell's zebras, Klingel (1967) found mean herd sizes ranging from 4,5—7,7 in various populations. Feist (1971) reported a mean herd size of 5,0 in feral horses *E. caballus* in the Pryor Mountain Wild Horse Range, U.S.A.

Of the 26 foals still with their maternal herds on 30 June 1973, nine (34,6%) were less than one year old and 17 (65,4%) were one to two years old. This reflects the poor foaling season (1972/73) when only nine foals were born, compared to 26 foals born the previous breeding season. In only one instance was a yearling still associated with his mother after the birth of a sibling. In Hartmann zebras, Joubert (1972) found that 61% of the foals were less than one year old and 39% one to two years old.

#### *Stability of the Social Organisation*

Once a breeding herd has become established, it remains stable over many years. This was also commented on by Klingel (1969a). Observations during the present study indicate that if a stallion dies or becomes disabled in some way, the breeding herd is usually taken over as a unit by a new stallion. A small number of exceptions occurred when breeding herds split up after the stallion was displaced by another (see "Herds splitting up").

The nine herds recorded by Klingel in the MZNP in 1965 and 1967 could still be identified when the present study commenced in June 1971.

One of these herds had not changed composition-wise since 1965. Two of the four mares in this herd died during 1972, but at the termination of the study the stallion and two remaining mares were still together — after at least eight years. Three further herds were the same in 1971 as in 1967. The composition of two of these herds changed during this study, but the other still had its original members at the termination of the study — after at least six years.

No adult mare left a breeding herd to join one of the original herds recorded by Klingel. In contrast, however, one adult mare who had been in the same herd in 1965 and 1967 had by 1971 joined a herd which had become established in the interim. It seems likely that once a mare has become firmly established as a member of a breeding herd, she remains with that herd until death. The rare instances of adult mares leaving breeding herds are exceptions to the rule.

Herd stallions were generally displaced when in poor condition and a stallion dying while in possession of a breeding herd was not recorded during the present study. Good physical condition of the stallion is therefore of primary importance in maintaining his position with a breeding herd. A herd stallion's length of tenure with a breeding herd varies considerably. At the one extreme a stallion, born in 1959 and already an established herd stallion in 1965, was still with his herd at the age of about 15 years at the termination of this study. At the other extreme a herd stallion (born in 1966) was displaced by a slightly younger bachelor at the end of 1973 when only about seven years old. He had been a herd stallion for at least 2,5 years, but probably not much longer. It is likely, however, that some physical disability had an influence in this case. A similar case occurred late in 1972 when a herd stallion was displaced and his herd subsequently split up (see "Displacement of the herd stallion").

#### *Social hierarchies and leadership*

Social hierarchies in the breeding herds of mountain zebras were reported by Klingel (1968) and Joubert (1972). That it occurs in all herds in the MZNP population was evident during the present study on some occasions. Leadership is defined here as: "an individual in the social unit coordinates and directs group movement by providing a focal point for the activity of the group" (Eisenberg 1965). Unlike the position in Burchell's zebra (Klingel 1967), no clearcut correlation between dominance and leadership was found in Cape mountain zebra during the present study. This tallies with what Joubert (1972) found in Hartmann zebra.

Klingel (1967) described a marching order according to rank in Burchell's zebra and stated that a similar situation exists in Cape mountain zebra (Klingel 1968). In the present study, this could be demonstrated in the smaller herds, but not in the larger ones.

In some of the smaller herds containing two or three mares, the social hierarchy was readily identifiable by noting the number of threat gestures

between the various mares and the reaction of the recipient. In herds containing up to five mares, the interpretation was not so clear. The larger herds are probably the longest-established ones and one herd was known to be stable for at least six years. In such a herd threat gestures between the adult mares are extremely rare as each individual apparently knows its relative position in the social hierarchy. In the absence of a correlation between dominance and leadership or in marching order according to rank, social hierarchies were extremely difficult to determine in these herds. Evidence of a social hierarchy was evident, however, in the occasionally observed threat gestures and associated behaviour, e.g. presumably lower-ranking mares leaving a dustbowl at the approach of a presumably higher-ranking mare.

The herd stallion is the highest-ranking individual in the herd. All mares submit to his threats and he is also able to herd the mares.

The influence of oestrus and the presence of new-born foals on the social hierarchy is by no means clear and should be investigated further. De Vore (1965) described low-ranking female baboons *Papio ursinus* rising in rank when they are in oestrus or have small young. In *Rhabdomys pumilio*, Marais (1974) found pregnant females aggressive towards all other mice. In Cape mountain zebras, oestrus and the birth of a foal probably changes the social hierarchy. On several occasions it was observed that low-ranking mares in oestrus threatened higher-ranking mares. This usually elicited a return threat by the higher-ranking mare a few minutes later. Mares with new-born foals are extremely aggressive towards the other members of the herd. This could probably lead to a temporary rise in the social hierarchy by such a mare.

Reproductive success *per se* is apparently not a prerequisite for social dominance. In one of the herds a seemingly barren and fairly young mare (born 1966/67) was dominant, even outranking an elderly mare who had foaled in the 1971/72 summer and two other young mares who foaled in the 1971/72 summer. In another herd with only two mares, one was clearly dominant and also initiated virtually all movements. She foaled during the 1971/72 summer. The other mare never initiated movements, always followed behind the dominant mare and her foal when the herd was moving and waited for the dominant mare to finish dust-bathing before she took her turn. The low-ranking mare foaled in the 1973/74 summer and her behaviour changed just prior to the birth of her foal. She threatened the previously dominant mare and her foal when they approached and also initiated group movements.

The establishment of a social hierarchy was clearly evident in the formation of a herd which was established in September/October 1971 when a five-year-old stallion successfully herded a *ca* 2.5-year-old mare which had left her maternal herd a few weeks previously. By January 1972 another young mare had been added to the herd and the original mare was observed threatening the new mare at all sightings of this herd. In April 1972 a third mare, from the same maternal herd as the original mare, also joined and from then onwards was threatened by the second mare. Al-

though lacking sufficient observations for quantitative analysis, the impression was gained that there were more threat gestures by the second mare to the third than by the first to the third. This may be explained by their common origin. It is possible that, even before joining the herd, the third mare knew her position in relation to the first mare. When the fourth mare joined a year later, the new mare was threatened by all three mares – possibly more by the second and third mares. In this case, too, the first mare and therefore the dominant one, was the leader in all movements initiated by the mares.

Leadership is by no means confined to mares. In a sample of 141 observed movements other than to water, the herd stallion initiated 46 (32,6%) and the mares 95 (67,4%) of the movements. Bearing in mind that the stallion:mare ratio in the breeding herds is 1:2,4 the data were subjected to a chi-square test and were found not to differ significantly from a 1:2,4 ratio ( $\chi^2=0,701$ ;  $df=1$ ;  $p>0,05$ ). Leadership is therefore regarded as random. In the case of Hartmann zebra which has virtually the same sex ratio as Cape mountain zebra in the breeding herds, Joubert (1972) reported that the stallion took the initiative in leading the herd in approximately one-third of his observations.

When a Cape mountain zebra stallion is not leading his herd, he usually brings up the rear or walks alongside his mares, which usually walk in single file. When moving from danger, the initiative is normally taken by a mare, usually the one with the youngest foal (Joubert 1972) and the stallion stays behind, facing the source of danger. When his herd has moved off, he follows but wheels around frequently to face the danger.

When a breeding herd approaches a water-hole, the stallion normally leads. In 40 observations, the herd stallion led 25 (62,5%) and a mare 15 (37,5%) times. This differed significantly from a 1:2,4 ratio ( $\chi^2=18,586$ ;  $df=1$ ;  $p<0,01$ ). Klingel (1968) stated that Hartmann zebra stallions led to water in 75% of his observations.

In a general discussion, Eibl-Eibesfeldt (1970) regarded social hierarchy as important because the high-ranking animal not only has a number of special advantages, such as being first at the feeding place or obtaining the best-possible shelter, but it may also assume the responsibility of leadership and of protecting the group against predators or of protecting one group member from another. Such an explanation does not account for the existence of a social hierarchy among mountain zebra mares. In these grazers, being first at a feeding locality is a virtually non-existing concept and defence is only performed by a stallion. Although defensive action by the stallion was not observed due to the lack of large predators in the MZNP, the behaviour of the stallion in this respect is similar to Burchell's zebra where active defence does occur (Kruuk 1972). Some other explanation is required for the existence of social hierarchies.

Crook & Goss-Custard (1972) listed the main processes occurring in the maintenance of social structures. They are (a) "competitive dynamics" leading to dominance rankings; (b) "integrative dynamics" comprising the effects of social facilitation, behavioural copying, follow-up responses, and

the simple control of individual and group affect to prevent group disintegration; and (c) "bonding dynamics" comprising behaviour that bonds individuals in various groups. Crook & Goss-Custard concluded: "The complexity of vertebrate societies increases to the degree to which all three processes are present and cofunctional".

A social hierarchy among the mares in *E. zebra* could therefore primarily be regarded as one of the mechanisms for the maintenance of the social structure.

#### *Displacement of the herd stallion*

Once a stallion has successfully established a herd or acquired an existing herd, he usually retains his position in that herd until old age or ill health enables a younger stallion to displace him.

Six stallions were displaced during the present study. In three cases the herd of the displaced stallion split up, but one of these stallions was able to retain a single mare from his previous herd. In the remaining cases the stallion was totally displaced and the entire herd taken over.

Old age or poor health were the reasons for three of the stallions being displaced. The old stallion which was displaced appeared in good physical condition, later formed a core group with another stallion (see "Bachelors") and died more than two years later. The two stallions which were in poor health when displaced were seven and nine years old respectively. They both appeared in good physical condition when displaced and their displacement at first seemed inexplicable. Within a few weeks following displacement the condition of both stallions deteriorated markedly, however. The nine-year-old stallion died of massive parasite infestation five months after being displaced. The condition of the seven-year-old stallion deteriorated for two months after being displaced, but he subsequently regained his former good condition and joined a core group of bachelors. When the study was terminated 18 months after this stallion had been displaced, he was still with the bachelor core group.

In the remaining three cases, the displaced stallions showed no signs of illness, but positive signs of fighting, indicating a violent displacement. One of these stallions was 10 years old and had been with his herd for about six years. The herd consisted of five mares and the stallion managed to retain one mare. The second stallion was 7,5 years old when displaced and had been a herd stallion for two years. The remaining stallion was about six years old and had been a herd stallion for one year.

When observed shortly after being displaced, each of these three stallions had wounds to the neck and one individual had the tip of an ear bitten off. This indicated severe fighting, possibly for possession of the mares. A single fight was observed during the present study, and vicious biting of the opponent was one of the main elements of fighting.

Habituation as described by Joubert (1972) in Hartmann zebras was not observed during the present study, but could represent an alternative



displacement mechanism, especially of old or weakened stallions. In habituation in Hartmann zebras a new stallion joined the herd of a stallion in poor condition. When the new stallion was challenged by the herd stallion, he was submissive and retired. Every approach by the new stallion elicited the same response by the herd stallion, but the aggression-eliciting distance was gradually reduced until the new stallion joined the herd. The herd stallion had therefore become habituated to the presence of the new stallion. Eventually the herd stallion could no longer keep up with the herd, which was then taken over by the new stallion. Klingel (1967) witnessed a possible similar case in Burchell's zebras, but did not record any aggression between the two stallions.

Except for the stallion who was displaced in August and later died, the other five recorded displacements took place between October and January. This coincided with the increase in sexual activity, as reflected by the foaling season.

### *Herds splitting up*

The long-term stability of Cape mountain zebra breeding herds discussed previously was also remarked upon by Klingel (1969a), who previously reported a similar condition in Burchell's zebras (1967). However, during the present study the splitting up of four breeding herds was recorded. Two of the herd stallions were old animals and one was in poor health. The fourth case of splitting up was probably accidental, one of the mares being temporarily absent from the herd when the herd stallion was displaced by a bachelor. This mare and the displaced stallion subsequently joined up and were still together at the termination of the study 20 months later.

Three of the four herds which split up were large, containing four or five mares each. This suggested that a herd involving a large number of mares cannot be maintained over a long period and that the bonds between individual mares in a large herd are not as substantial as in smaller herds (see "Social hierarchies and leadership").

The splitting up of the herd belonging to an old stallion took place in stages (Fig. 5). In the other case the old stallion had a single mare, filly and a colt in his herd. The filly was captured and removed in October 1971 and the colt left the herd a few weeks later. The old stallion deserted his mare two months later and joined a bachelor group, but the mare remained solitary until the termination of the study 2,5 years later. The advanced age of the mare could have resulted in a permanent anoestrus, which could account for her desertion by the stallion.

In the case of the stallion in poor health, a bachelor took over two of the mares in the herd. The two remaining mares were alone for a few weeks, even after the displaced stallion had joined a bachelor group, and were eventually acquired by another bachelor. Joubert (1972) described a case in Hartmann zebras where a bachelor succeeded in displacing a herd stal-

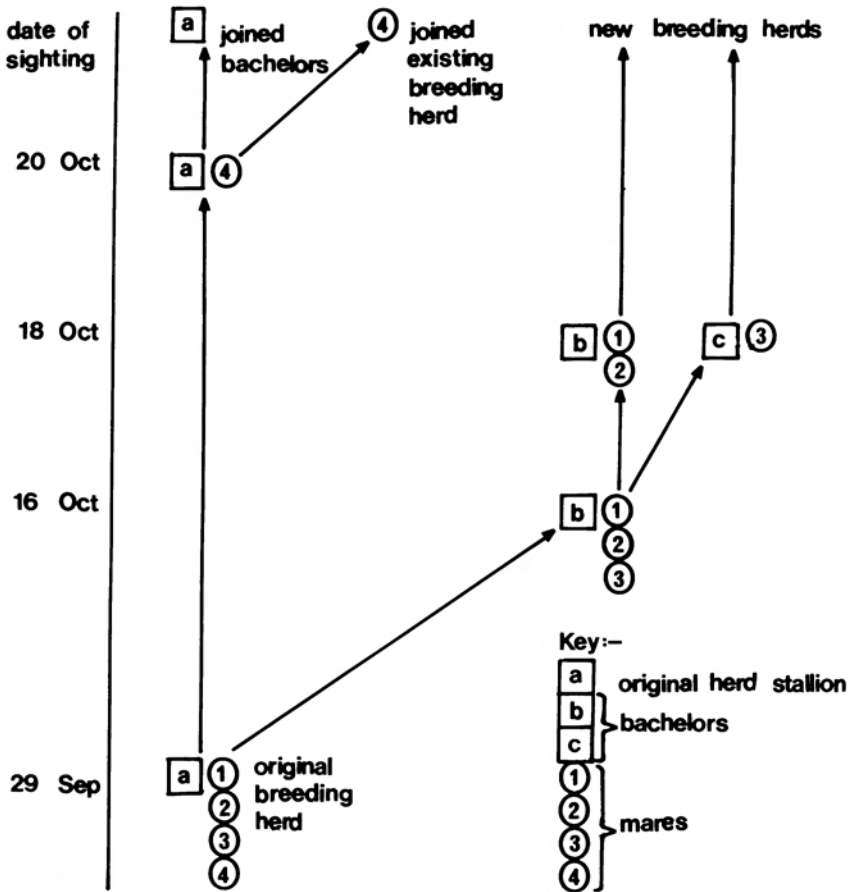


Fig. 5. Diagram of the splitting up of a Cape mountain zebra breeding herd in the Mountain Zebra National Park during October 1971.

lion, but was interested in only two of the mares and actively herded them, while trying to keep the remaining mares away. After a week he was no longer successful in keeping the others away and the two sections of the original herd rejoined. It is likely that in such a case the mares which were herded by the new stallion were in oestrus. The bond between the mares was of paramount importance in maintaining the cohesion of the breeding herd and the herding of the stallion was incidental. In the Cape mountain zebra herd the new stallion was either successful in keeping the remaining mares away, or the bonds between the mares were not strong enough to prevent the herd from splitting up permanently.

Splitting up of one other herd in the MZNP can probably be explained by deduction. This herd, described by Klingel in 1965, contained four adult mares. Two of these mares died during a severe snowfall in August 1971 before their herd affinities could be determined. The remaining two were subsequently encountered, each in a different herd.

### *Mare temporarily leaving herd*

Members of a breeding herd usually maintain close proximity. During grazing, individuals may occasionally move gradually away from the herd, even as far as a few hundred metres, but they always return to the main body of the herd after a shorter or longer period. However, in a number of instances a mare was encountered a few kilometres from her herd. In most cases this was probably due to the mare losing contact with her associates by grazing too far or by sleeping while the herd moved on. These observations were rare and the mares soon rejoined their herds. At least two mares, however, showed a distinct tendency for leaving their herds temporarily.

Detail on specific cases may require elucidation. Herd C contained five adult mares until it split up in October 1972. In the preceding 18 months this herd had been recorded 78 times, mare C<sub>2</sub> and her foal(s) being absent on 11 occasions (14% of the sightings). They were usually absent for a few hours. On one occasion they were seen steadily walking away from the grazing herd and on another they were not with the herd when first encountered but had returned a few hours later. In January 1972 they were apparently absent for a few days. Mare C<sub>2</sub> was in oestrus at the time and was mated by a stallion from another herd. The stallion did not attempt herding her. Mare C<sub>2</sub> and her foal were consistently absent from 16 October onward. By 30 October the herd stallion had been displaced by a bachelor. Mare C<sub>2</sub> and her foal were probably absent when this occurred and they were joined by the displaced stallion during November 1972. Six weeks after the herd split up another of the mares and her foal temporarily joined the displaced stallion and mare C<sub>2</sub>, but they soon returned to their original herd. Mare C<sub>2</sub> was at least 16 years old when the present study was initiated.

In 1965, mare C<sub>2</sub> was a member of a herd which in addition contained two other adult mares. In 1967 a further two mares had been added. In all probability, the bonds between mare C<sub>2</sub> and the other mares were weak, the herd size being the maximum recorded (five mares). However, the other two original mares did not show a tendency for leaving the herd.

Herd V inhabited one of the rugged kloofs of the Bankberg and was only recorded 27 times. On nine occasions mare V<sub>2</sub> and her foal were not with the herd (33% of the sightings). Mare V<sub>2</sub> was one of the oldest individuals in the MZNP population and was at least 18 years old when the present study was initiated. In 1965 and 1967 mare V<sub>2</sub> was in a herd with three other adult mares. Two of them died in August 1971 and the other was seen with another herd during the present study. The two other mares in the same herd as mare V<sub>2</sub> during the present study were both young, one only joining the herd in December 1971. The bonds between mare V<sub>2</sub> and these two mares may therefore have been weak.

Young mares which have just left their maternal herds usually do not stay with the first stallion or herd encountered. This is similar to the behaviour of Burchell's zebra, where Klingel (1969b) reported: "The young

mare normally does not stay with the stallion who abducts her. When she has been separated from her original family, the fight over her continues and only ceases when oestrus ends. With the next oestrus it all starts over again up to the age of 2 to 2½ years, when the mare becomes a permanent member of a family". In the present study a single case was recorded of a young Cape mountain zebra mare consistently returning to the same herd. She was taken into a newly-formed herd in January 1972 and remained with this herd for a few months. She left the herd on a number of occasions between May and December 1972, being seen alone and with various bachelors for varying lengths of time. From January to May 1973 she was back with the original herd, but from the end of May to December 1973 she was consistently with the same bachelor. At the beginning of January 1974 she was once again temporarily back with the original herd.

#### *Stallion temporarily leaving herd*

Whenever one breeding herd comes in proximity to another breeding herd or bachelor group, the stallion of the breeding herd leaves his herd to perform a challenge ritual with the stallion of the other breeding herd or with the bachelors. This activity usually takes place within 100 m-300 m of his own herd. After the challenge ritual the stallion usually grazes or walks directly back to his herd, usually rejoining his herd within 10–20 minutes. However, occasionally herd stallions were encountered with bachelor groups when their own breeding herds were not in sight. This occurred in 25 out of 467 sightings of bachelor groups (5,4% of all sightings). The herd stallion lingered with the bachelors for a longer time and participated in the activities of the bachelor group, such as grazing, drinking and dust-bathing.

Nine of the 21 herd stallions were with bachelor groups at various sightings. An analysis of the frequency of absence of the herd stallion from his herd is shown in Table 4, in which only breeding herds sighted more than 50 times are included. Five of the 16 stallions represented in the table were with their herds at all sightings. A further nine stallions were away occasionally, but never for more than 4% of the sightings. The two remaining stallions were absent from their herds on 12,5% and 14,3% of the sightings respectively and this will be discussed briefly.

**Herd C:** the herd stallion was not with his herd in 12,5% of the sightings, being absent for at least 4,5 hours on one occasion. He was later displaced by a bachelor, but joined up with a mare from his original herd, leaving her once only in 36 subsequent sightings.

**Herd L:** the herd stallion was in the company of the same bachelor core group on 12 sightings, once being about 1,5 km from his herd. A colt from this breeding herd joined the bachelor group shortly after leaving the herd, suggesting that he knew at least one of the members. It is likely, therefore,

that at least one of the bachelors had originated in herd L, which could account for the degree of attachment that the herd stallion showed to this particular bachelor group.

Table 4

*Frequency distribution of the number of times a Cape mountain zebra herd stallion was absent from his herd.*

Herd	Total Sightings	Stallion Absent	Percentage Absence
L	147	21	14,3
C <sub>a</sub>	80	10	12,5
O	82	3	3,7
J	84	3	3,6
M	96	3	3,1
H	137	4	2,9
D	87	2	2,3
N	101	2	2,0
I	124	2	1,6
E <sub>b</sub>	74	1	1,4
S	99	1	1,0
C <sub>b</sub>	54	0	0
E <sub>a</sub>	79	0	0
E <sub>c</sub>	72	0	0
F	72	0	0
Q	134	0	0

C<sub>a</sub> – herd C before herd stallion was displaced by bachelor

C<sub>b</sub> – herd C after herd stallion was displaced by bachelor

E<sub>a</sub> – herd E before it split up and herd stallion was displaced

E<sub>b</sub>E<sub>c</sub> – two sections of original herd E taken over by bachelors.

#### *Adult mares joining other herds*

During the present study no case of an adult mare leaving her herd and joining another herd was recorded, but a mare from one of the herds that split up joined an existing herd. In contrast, however, Klingel's records revealed that at least one adult mare left her herd and joined another herd. The herd which she deserted still existed when the present study was initiated, while the herd she joined had become established after 1967. She was an extremely old mare and died in 1972. Another possible case concerns two mares who were in the same herd in 1967, but in different herds in 1971. The stallion who had been with the herd in 1967 had died in the interim and it is possible that the herd had split up, rather than that one of the mares had left the herd and had joined another.

Theoretically, if a mare lost contact with her herd in some way, like grazing away too far and not noticing her herd moving off in a different direction, she may be taken into another breeding herd. However, in the relatively small MZNP the chances of her later meeting up with her original herd are good, and she would probably rejoin it. A mare leaving her herd and permanently joining another herd occurs so infrequently that it may be disregarded when the parameters of social organisation for the MZNP population are discussed.

*Foals leaving their maternal herds*

During the present study 33 foals left their maternal herds permanently. Another, a filly of *ca* 10 weeks old, was adopted by a mare in another herd.

Eighteen of the foals leaving their maternal herd were born during the present study period and their exact ages are therefore known. The ages at which these foals left their maternal herds are given in Table 5. The mean age at leaving maternal herds did not differ significantly for colts and fillies ( $t=0,7729$ ;  $df=16$ ;  $p>0,05$ ) and they were therefore lumped, giving a mean age of 22,3 months (range 13–27 months).

Table 5

*Age (in months) at which Cape mountain zebra foals in the Mountain Zebra National Park left their maternal herds.*

SEX	n	AGE			
		mean	range	S.D.	C.V.
Colts	7	23,3	16-27	4,54	19,5%
Fillies	11	21,7	13-26	4,56	21,0%
Total	18	22,3	13-27	4,63	20,8%

Eight of the known-age foals leaving their maternal herds did so after the birth of a sibling. The ten other known-age foals left their maternal herds even though no sibling had been born. The mean age at leaving the herd for these two groups is given in Table 6. The means of these two groups did not differ significantly ( $t=0,276$ ;  $df=16$ ;  $p>0,05$ ).

Fifteen of the 33 foals leaving their maternal herds did so after the birth of a sibling, at an average of about four months after the birth of the new foal. The recorded range varied from a few days to 14 months after the birth of the sibling.

Of the 33 foals leaving their maternal herds, 24 did so during the summer and nine during the winter. Significantly more foals left their maternal

Table 6

*Age (in months) at which Cape mountain zebra foals in the Mountain Zebra National Park left their maternal herds after the birth of a sibling or if no sibling had been born.*

FOAL LEAVING HERD	n	AGE			
		mean	range	S.D.	C.V.
After birth of sibling	8	23,0	16-27	3,92	17,0%
No sibling born	10	21,8	13-27	5,02	23,0%

herds during the summer than during the winter ( $\chi^2=6,818$ ;  $df=1$ ;  $p<0,01$ ).

The foals left the herds of their own accord and were not forced to do so by the herd stallion. The reverse held true, as the stallion actively tried to prevent the foals from leaving.

#### *Fillies*

Fillies appear to leave their maternal herds during their first oestrus. Although actual leaving of the herd was not witnessed during the present study, several fillies which were encountered within a day or so after leaving their maternal herds, were in oestrus, displaying the characteristic oestrus posture of the young mare. They were seen wandering alone, with various breeding herds, or with bachelor groups.

The older fillies were taken up into existing breeding herds or were successfully herded by a bachelor within a few weeks or months of leaving their maternal herds. Younger fillies were usually solitary or stayed with bachelor groups much longer before being taken up into existing breeding herds or being successfully herded by a bachelor.

Of two 2,5-year-old fillies, one was taken up into an existing breeding herd within a week of leaving the maternal herd, the other was successfully herded by a bachelor two months after leaving the maternal herd.

A 16-month-old filly leaving her maternal herd joined a bachelor core group after six months, where she remained for about one year until successfully herded by one of the bachelors in the group when she was 34 months old. A 13-month-old filly leaving her maternal herd was only successfully herded by a bachelor when she was 24 months old.

Three of the 14 fillies leaving their maternal herds were initially recorded returning to the herd for short periods.

In Burchell's zebra, Klingel (1967 and 1969b) described fillies in their first oestrus being abducted from their maternal herds by bachelors. The herd stallion tried driving the bachelors away, but many bachelors were usually present (18 in one case) and in all cases observed by Klingel, the

stallion was unable to prevent the abduction of the filly. The same could conceivably occur in Cape mountain zebra.

In Hartmann zebra, Joubert (1972) described the mare vigorously trying to expel her foal from the herd at the age of 14–16 months, prior to the birth of a sibling. Mare-foal aggression was only rarely observed in Cape mountain zebras during the present study and then only in relation to weaning. Joubert further described mares other than the mother trying to expel a filly in her first oestrus from the herd, but similar attempts were not observed in Cape mountain zebras during the present study.

### *Colts*

Cape mountain zebra colts leave their maternal herds at about the same age as the fillies (Table 5). The stallion actively tries to prevent their leaving. In three observations during the present study the herd stallion broke off naso-nasal contact between a colt from his herd and a bachelor by running between them and herding the colt back. In one observation nine bachelors were grazing near a breeding herd and a 2,5-year-old colt from the herd was gradually grazing towards one of the bachelors. When the colt reached the bachelor, they made naso-nasal contact but the herd stallion approached and ran between them, kicking at the bachelor as he passed, and herded the colt back.

A colt of 27 months left his maternal herd when the herd stallion was displaced by a bachelor, probably being forced to do so by the bachelor. The colt was seen with the displaced herd stallion in a bachelor group shortly afterwards, indicating no aggression between the herd stallion and the colt. Klingel (1967) noted a similar case in Burchell's zebra.

Seven of the 16 colts which were recorded leaving, were again seen with their maternal herds for short periods after varying intervals. One of these colts left his maternal herd in March 1972 when *ca* two years old. He was recorded back with the herd in May 1972, June 1972, January–February 1973, August 1973 and January 1974. He usually remained with the herd for a few days and was tolerated, but ignored. The only aggression recorded towards him was in June 1972 when he was threatened and charged by his mother. He moved off a few paces but remained with the herd. Another colt briefly rejoined his maternal herd eight months after first leaving. These cases may illustrate the long-term effect of individual recognition in the social organisation.

After leaving their maternal herds, the colts roamed singly or in unstable groups loosely associated with bachelor core groups.

Klingel (1967) regarded the following factors as being most important in Burchell's zebra colts leaving their maternal herds:

1. The mother of the colt has a new foal, which essentially breaks the bond between the mare and the older foal.
2. There are no contemporaries in the herd to act as playmates.
3. A bachelor group with suitable playmates is in the vicinity of a breeding herd.



Joubert (1972), however, postulated some other drive, probably innate, that compels the young stallion to leave his maternal herd and join the bachelor population. It may be the case, but the great variation in the age at which colts leave their maternal herds could indicate external factors, rather than an innate drive. The tendency for the colts to leave may be due to a combination of inherited and external factors.

#### *Formation of new breeding herds*

When a sexually mature filly leaves her maternal herd or when a filly which has left her maternal herd earlier becomes sexually mature (usually when about two years old), she is either taken up in an existing breeding herd or actively herded by a bachelor to form a new breeding herd. Fourteen young mares and three mares from a herd which had split up became available in this way during the present study. Eight new herds were formed. Two of the bachelors which successfully herded mares during October 1971 to form new herds were born in 1966/67 and were therefore about five years old at the time. Joubert (1972) demonstrated that Hartmann zebra stallions only reach their maximum mass around seven years of age. The same probably applies to Cape mountain zebra stallions. The older (and larger) bachelors therefore have a physical advantage when competing with younger (and smaller) bachelors for any available mare. The oldest bachelors (apart from displaced stallions) were about five years of age and it is doubtful whether a younger bachelor would be able to herd a mare successfully in the face of competition from the older bachelors.

Herd S is a good example of the formation of a new breeding herd. A 2,5-year-old filly which had left her maternal herd around August 1971 was seen with various breeding herds and bachelor groups until October 1971, when she was successfully herded by a five-year-old bachelor. In January 1972 a further filly was added to the new herd and in April 1972 another 2,5-year-old filly from the same herd as the first one was added. In April 1973 a further 2,5-year-old filly was added. The first foal in this herd was born to the original mare about February 1974, 28 months after the formation of the herd.

The herd which split up in October 1971 set off a chain of events (Fig. 5). One of the mares was taken up into an existing herd, two of the others were successfully herded by a five-year-old bachelor to form a new herd and the remaining mare and her one-month-old foal were herded by a *ca* 5,5-year-old bachelor.

Newly-formed breeding herds are often unstable and the stallion is occasionally displaced after a few weeks or months. If the stallion had been a member of a bachelor core group, he rejoined the group after being displaced. In Hartmann zebra, Joubert (1972) found that young stallions, especially after their first herding activity, may lose their mares to older, more experienced stallions who may or may not have their own breeding herds. When a young Hartmann zebra stallion lost his mares, he normally rejoined his original bachelor group.

## *Bachelors*

A 1:1 sex ratio at birth and a social organisation in which one adult stallion usually has more than one mare in his herd results in a surplus of stallions, which is accommodated in bachelor groups. Most stallions in the bachelor groups are youngsters which have left their maternal herds but have not yet attained mares of their own. The few displaced herd stallions also join these bachelor groups.

There is a constant coming and going in the bachelor population as young stallions join and older stallions leave when acquiring mares and becoming herd stallions. During the present study the number of bachelors varied between 24 and 27, or 17%–20% of the population.

Additions to the bachelor population during the present study comprised two stallions introduced from the Kamanassie and Kouga Mountains respectively, four displaced herd stallions and 13 young stallions which had just left their maternal herds. Losses from the bachelor population were three young stallions which died (two during a severe snowfall in August 1971), two displaced stallions which died (four and 27 months respectively after being displaced) and 12 which became herd stallions. Four of these bachelors displaced herd stallions in existing herds and the others acquired young mares which had just left their maternal herds or mares from the herds which split up. The bachelor population therefore serves as a reservoir from which herd stallions are supplied.

The structure of bachelor groups is much less rigid than that of the breeding herds and no well-defined herds could be distinguished during the present study. In general, certain core groups could be identified as groups remaining stable over long periods in contrast to individuals which joined these core groups for varying lengths of time and also formed their own unstable groups. As no pattern of association was readily discernible in the population, the field data were subjected to a Principal Components Analysis to achieve an ordination of individuals in the population.

Principal Components Analysis (PCA) is a form of factor analysis and was discussed by Gittins (1969), while a more detailed account can be found in Seal (1968) and Cooley & Lohnes (1971). The PCA was carried out with the aid of an IBM 360/40 digital computer of the Computer Centre, University of Pretoria. The programme used was written by Dr. J. W. Morris\* and was made available by Prof. J. O. Grünow.\*\*

The 31-month observation period was divided into nine periods of three months each and one four-month period. The three-month periods were subjected to a Principal Components Analysis. The individual bachelors were regarded as the entities and the observations as the attributes. The

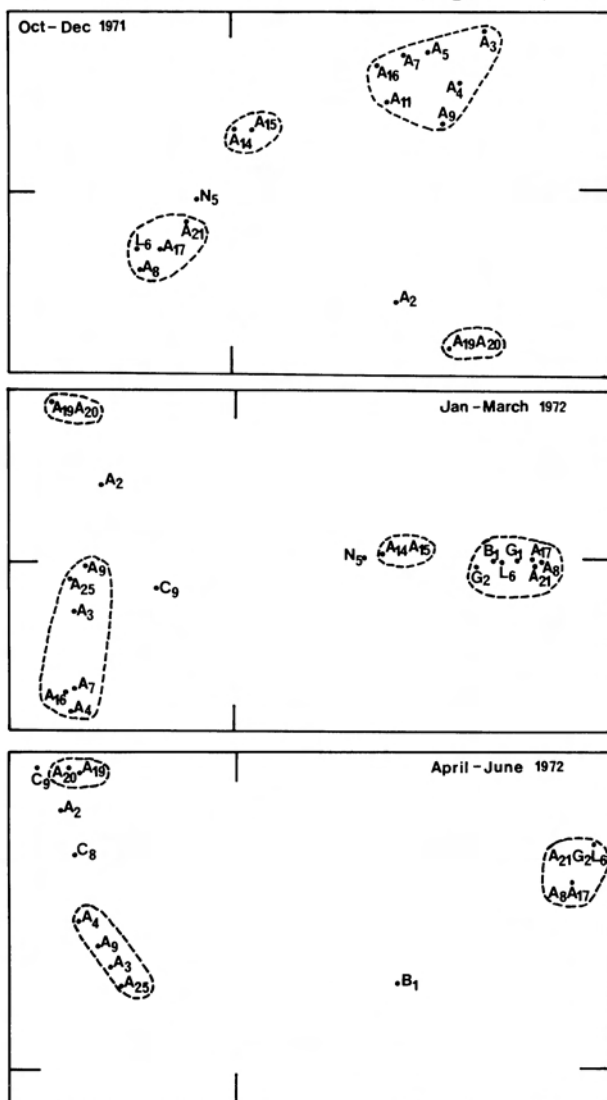
---

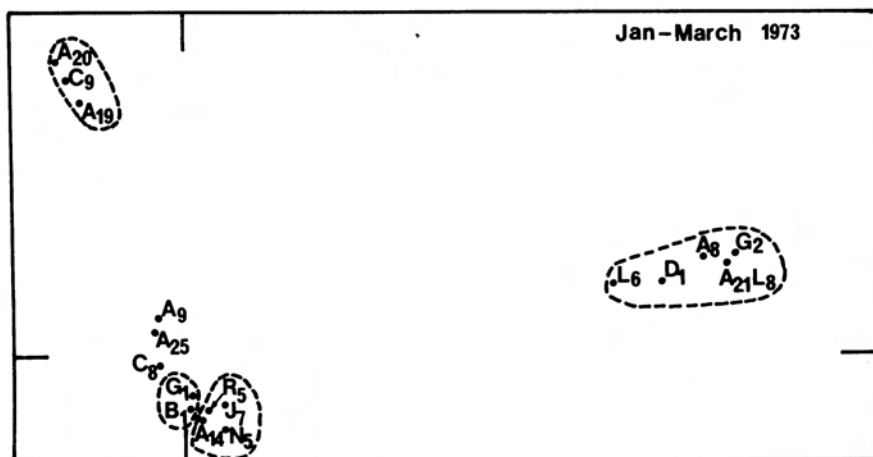
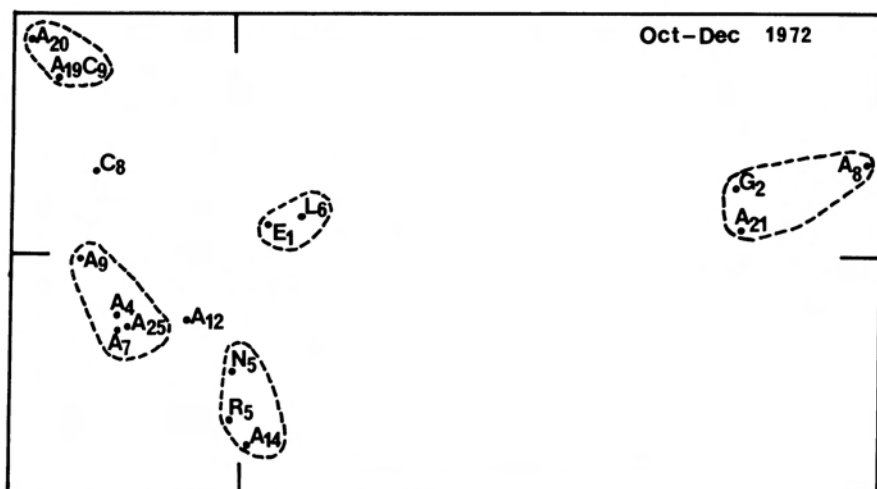
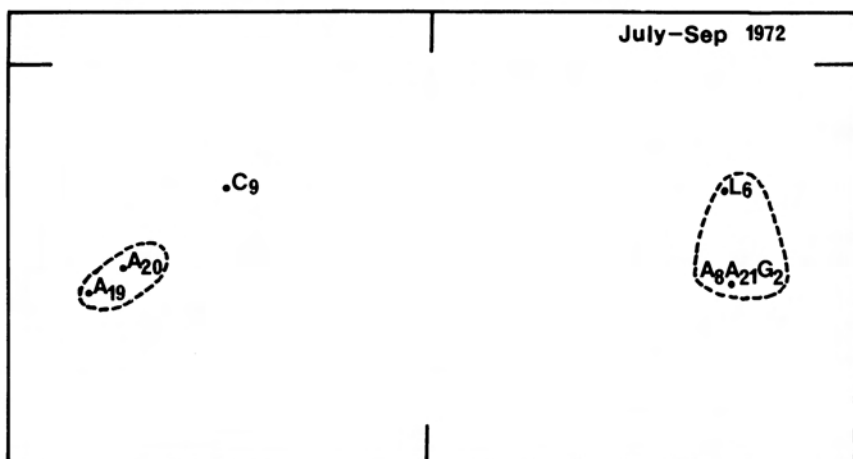
\* *Botanical Research Institute, P. Bag X101, Pretoria 0001.*

\*\**Dept of Plant Production, Faculty of Agriculture, University of Pretoria, Pretoria 0002.*

four-month period (June–September 1971) contained only 19 sightings with only five individuals being sighted five or more times and this period is therefore not included in the PCA (see later).

The position of the individuals (geometrical distances) was plotted on the X and Y axes in relation to the first two components respectively (Theron 1973). When the results were plotted it became evident that the individuals of which there were only a few sightings during a three-month period were grouped around the zero mark, even if there was no association between individuals. An arbitrary decision was therefore made to ignore all individuals with less than five sightings in a given period. As a result, not all individuals are plotted in all consecutive periods. Good clustering was obtained for the other individuals (Fig. 6 a–c). Groups of indi-





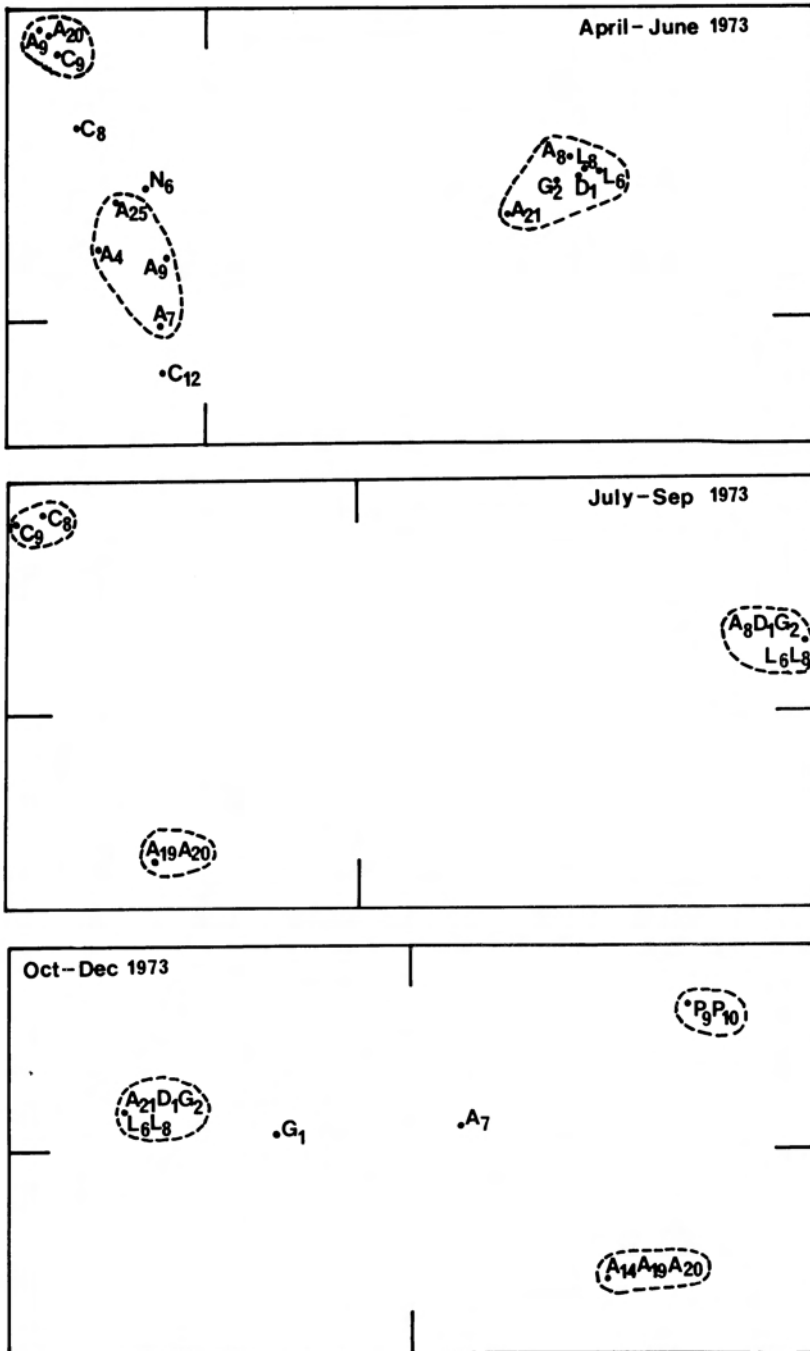


Fig. 6. a-c. Ordination of Cape mountain zebra bachelors in the Mountain Zebra National Park in three-month periods (October 1971 to December 1973) to illustrate association between individuals.

viduals were defined arbitrarily by means of isolines of association. The graphic illustrations refer to temporal association between individuals and do not reflect actual spatial distribution. An individual represented by an isolated dot was usually not a "loner" but rather was seen with different groups of individuals, showing no preference for, or association with any of them. The first three components, except for the period October–December 1972 (43.7%) account for more than 50% of the variation in the different observations (Table 7).

### *Core groups*

One possible and three definite core groups could be recognised. One core group consisted of  $A_8A_{17}A_{21}$  when first seen in June 1971. During October–December 1971 this group was joined by  $L_6$  which had just left his maternal herd. During January–March 1972 this group was joined by  $G_2$  which had just left his maternal herd,  $B_1$  whose herd had split up and  $G_1$  (father of  $G_2$ ) who had deserted his single mare. Stallions  $B_1$  and  $G_1$  then split off and formed their own core group which remained stable until  $B_1$  died 18 months later. In August 1972 stallion  $A_{17}$  left the group and became a herd stallion. During October–December 1972 bachelor  $L_6$  left the group to join a displaced stallion, but returned when the displaced stallion died. During January–March 1973 the group was joined by  $D_1$ , a displaced stallion, and  $L_8$ , a young mare from the same maternal herd as  $L_6$ . This group remained constant until  $A_8$  left in November 1973 to become a herd stallion. Bachelor  $A_{21}$  left for the same reason in January 1974 (taking  $L_8$  with him). At the end of the present study the original members of this group had therefore left, but the group as such still existed, albeit with other members.

Core group  $A_{14}A_{15}$  was first seen in June 1971 and remained constant until October 1972 when  $A_{15}$  became a herd stallion. Bachelor  $A_{14}$  then formed a fairly stable group with  $N_5R_5$  for about one year until he joined core group  $A_{19}A_{20}$  in November 1973 ( $N_5$  had been with  $A_{14}A_{15}$  during January–March 1972).

Bachelors  $A_{19}A_{20}$  were a core group which stayed together throughout the study period. They were joined by  $A_2C_8C_9$  for a short period in April–June 1972. In October–December 1972 bachelor  $C_9$  returned and remained with  $A_{19}A_{20}$  until July–September 1973 when  $C_8$  rejoined the group. Bachelors  $C_8C_9$  left the group shortly afterwards. By October–December 1973  $A_{19}A_{20}$  had been joined by  $A_{14}$ .

Bachelors  $A_4A_7A_{25}$  represented a further probable core group. In October–December 1971 they were associated with  $A_3A_9A_{11}A_{16}$ , which all became herd stallions during the study. They were fairly closely associated until April–June 1972. By April–June 1973 bachelors  $A_4A_7A_9A_{25}$  were still associated. This group was rarely encountered on the Rooiplaat plateau and apparently preferred the rugged Bankberg area, where they

Table 7

*Value, component and cumulative component of the first four Eigen vector components in a PCA ordination of Cape mountain zebra bachelors during nine three-month periods in the Mountain Zebra National Park*

PERIOD		COMPONENT			
		C <sub>1</sub>	C <sub>2</sub>	C <sub>3</sub>	C <sub>4</sub>
Oct-Dec 1971	Value	13,847	9,784	8,984	5,914
	Component	22,334	15,780	14,490	9,539
	Cumulative component	22,334	38,114	52,604	62,143
Jan-March 1972	Value	20,842	9,652	8,190	4,809
	Component	28,165	13,043	11,068	6,499
	Cumulative component	28,165	41,208	52,276	58,775
April-June 1972	Value	13,574	7,285	4,731	4,343
	Component	28,279	15,176	9,857	9,047
	Cumulative component	28,279	43,456	53,312	62,360
July-Sept 1972	Value	7,355	4,914	2,946	2,445
	Component	31,977	21,364	12,807	10,632
	Cumulative component	31,977	53,341	66,148	76,780
Oct-Dec 1972	Value	10,998	8,388	5,976	5,945
	Component	18,963	14,463	10,303	10,250
	Cumulative component	18,963	33,426	43,728	53,978
Jan-March 1973	Value	18,783	10,004	7,259	7,025
	Component	26,832	14,292	10,370	10,035
	Cumulative component	26,832	41,124	51,493	61,529
April-June 1973	Value	16,715	8,624	5,400	3,921
	Component	30,954	15,970	10,000	7,262
	Cumulative component	30,954	46,925	56,925	64,187
July-Sept 1973	Value	10,749	7,543	5,527	1,608
	Component	38,390	26,941	19,740	5,744
	Cumulative component	38,390	65,331	85,071	90,815
Oct-Dec 1973	Value	7,273	5,991	5,450	3,337
	Component	23,460	19,325	17,580	10,765
	Cumulative component	23,460	42,784	60,365	71,130

were occasionally seen. The resulting number of sightings is therefore small and precludes any definite deductions.

These were the only core groups which could be demonstrated. The paucity of observations on some of the remaining individuals which inhabited the more inaccessible areas of the Park preclude any conclusions on possible further core groups.

In general, it appeared that core group individuals were mostly the senior bachelors prior to becoming herd stallions.

#### *Non-core group individuals*

Non-core group individuals are usually the young stallions which have just left their maternal herds.

Bachelor  $N_5$  was an example of a non-core group individual. He left his maternal herd in November 1971. In November–December 1971 he was seen with a total of 14 of 22 bachelors in various combinations in six observations, but showed some preference for core group  $A_8A_{17}A_{21}L_6$ . During January–March 1972 he was seen with all 23 bachelors in various combinations in 18 observations, but showed some preference for core group  $A_{14}A_{15}$ . During April–June 1972 and July–September 1972 he was seen with 12 of 24 and five of 17 bachelors in four and three observations respectively, all three observations in July–September 1972 being with  $A_{14}A_{15}R_5$ . During October–December 1972 he showed association with  $A_{14}R_5$ , bachelor  $A_{15}$  having become a herd stallion. In January–March 1973 this group was joined by  $J_7$ . During April–June 1973 bachelor  $N_5$  was seen with a total of 14 of 25 bachelors in four observations, three of which being with  $A_{14}J_7R_5$ . In a total of 28 observations in July–September 1973, bachelor  $N_5$  was not seen; neither were  $A_{14}J_7R_5$ . In October–December 1973 bachelor  $N_5$  was seen three times, twice with  $J_7$ . Although  $N_5A_{14}R_5$  showed association for at least six months, this was rather short when compared to the core groups discussed previously.

#### *Family ties and the formation of core groups*

Bachelors  $C_8$  and  $C_9$  are two further non-core group individuals, which may have been in the process of forming a core group.

Bachelor  $C_9$  left his maternal herd in December 1971–January 1972. During January–March 1972 he was seen with a total of 21 of 23 bachelors in 12 sightings, but showed possible slight preference for  $A_4A_7A_{15}$ . Bachelor  $C_8$  left the same maternal herd in March 1972. During April–June 1972, bachelors  $C_8C_9$  and  $A_2$  showed association with  $A_{19}A_{20}$ . From July–September 1972 to January–March 1973, bachelor  $C_9$  showed close association with  $A_{19}A_{20}$ , but  $C_8$  did not and was seen with various other bachelors. During October–December 1972, bachelor  $C_8$  was seen with 16 of 24 bachelors in seven observations, being with  $A_{19}A_{20}C_9$ , on three occasions, and also joined his mother on various occasions. During April–



June 1973, bachelor  $C_8$  showed some association with  $A_{19}A_{20}C_9$ , but by July–September 1973 bachelors  $C_8C_9$  had formed a close association and showed no association with  $A_{19}A_{20}$ . During November 1973–January 1974 they had been joined by  $A_{25}$  and  $C_{12}$ , the brother of  $C_8$ .

Bachelors  $C_8$  and  $C_9$  were contemporaries in the same maternal herd and left the herd shortly after each other. They were seen together irregularly during an 18-month period before finally associating with each other over a longer period, even though  $C_9$  had consistently been with a core group for about a year. This raises the question of the role of family ties in bachelor groups and in the formation of core groups.

An Index of Association between two individuals can be calculated by the following formula:

$$\text{I.A.} = \frac{2c}{a+b}$$

$a$  = no. of sightings of individual A

$b$  = no. of sightings of individual B

$c$  = no. of sightings of A and B together.

An Index of Association of 1,00 indicates complete association on all sightings and an Index of Association of zero indicates no association at all. A similar index was used by Schaller (1972).

Two further pairs of bachelors from the same maternal herd were observed. Of the one pair,  $N_5$  left his maternal herd in November 1971 and  $N_6$  left the same herd in April 1973. After  $N_6$  had joined the bachelor population, he was seen on 15 occasions, four of these sightings being with  $N_5$ , who was seen on only two further occasions during the same period. For  $N_5$  and  $N_6$ , the I.A. = 0,38 which indicates no real preference for each other. Of the other pair,  $R_5$  left his maternal herd between November 1971 and February 1972 and  $R_6$  left the same herd in February 1973. After  $R_6$  had joined the bachelor population he was seen on eight occasions and  $R_5$  on 10 occasions. They were together on seven occasions, I.A. = 0,78, indicating a fairly close association.

Three further cases of possible sibling association concern fillies and young stallions. Filly  $L_8$  left her maternal herd immediately on the death of her mother in July 1972. She was seen with various herds up to December 1972, but by January–March 1973 had joined core group  $A_8A_{21}D_1G_2L_6$ , with which she remained about one year until being herded by  $A_{21}$ . Bachelor  $L_6$  had left the same maternal herd in November 1971 and had joined the core group virtually immediately.

Filly  $C_{14}$  left her maternal herd in January 1973 and during April to September 1973 was seen on six occasions, five times with  $C_{12}$  (who was seen three further times), giving an I.A. = 0,71 indicating fairly close association.

Bachelor  $P_{10}$  left his maternal herd on a few occasions in March 1973 but had returned by April 1973. On 18 May 1973 he was seen away from

the herd, accompanied by filly P<sub>9</sub>. They were seen together on seven occasions in October–December 1973 (I.A. = 1,00).

It has been demonstrated that the core group members are usually the senior bachelors prior to becoming herd stallions, while the non-core group individuals are usually the young stallions which have just left their maternal herds. Close association over longer periods of time probably develops among individuals and groups of these stallions in due course, resulting in new core groups. On leaving his maternal herd, a young stallion could join a core group if a sibling was a member, as may have been the case with L<sub>6</sub>, or roam unattached until forming a long-term association with a sibling (such as C<sub>8</sub>C<sub>9</sub>) or another individual or group. Siblings which leave the herd simultaneously probably remain associated and could become a core group.

With continued research the family ties of all bachelors in the population should be known within the next few years and problems encountered in explaining the social relationships should be solved.

### *Social hierarchy and leadership*

No social hierarchy could be determined in the various bachelor groups. As only core groups remain stable over long periods of time, definite social hierarchies could conceivably only develop in core groups. The association between non-core group individuals is probably too brief for the development of any social hierarchy. However, even in core groups no social hierarchy was readily evident. Joubert (1972) described a "silent" hierarchy in Hartmann zebra bachelor groups normally related to size and age, with individuals of the same age and/or same size acquiring the same position in the hierarchy. Only one observation which suggested a possible similar "silent" hierarchy in Cape mountain zebra was made during the present study.

Bachelor L<sub>6</sub> was about two years old when he left his maternal herd in November 1971 and joined core group A<sub>8</sub>A<sub>17</sub>A<sub>21</sub> virtually immediately. Bachelor G<sub>2</sub>, who was 3,5 years old and larger than L<sub>6</sub>, joined the same core group in January 1972. On 23 February 1972 a single observation was made of L<sub>6</sub> threatening the larger G<sub>2</sub>. If a "silent" hierarchy existed in this core group, L<sub>6</sub> would obviously have been the lowest-ranking individual, being the youngest, smallest and latest to join this core group. When G<sub>2</sub> joined, he would automatically have been the lowest-ranking individual which may account for the threat gesture by L<sub>6</sub>. (The previous day L<sub>6</sub> had threatened A<sub>14</sub>, a member of another core group and older and larger than L<sub>6</sub>, when A<sub>14</sub>A<sub>15</sub> approached the group that contained L<sub>6</sub>). Although L<sub>6</sub> and G<sub>2</sub> remained in the same core group for about two years, no other threat gestures were observed between them.

Social hierarchies may not exist among bachelors in this population. If they do exist, however, the possible mechanisms of the formation of core groups, discussed previously, would ensure that these core groups are es-

tablished over rather long periods of time. The members would therefore know their position in a social hierarchy and activities which maintain the hierarchy would be subtle or non-existent. The hierarchy would therefore be virtually impossible to discern.

Core groups are dynamic as older members leave to become herd stallions and younger members join. There could conceivably be no need for the vigorous establishment and maintenance of a social hierarchy as an individual would passively drift upwards gradually in the hierarchy as older members leave and young ones join.

No consistent leadership by any individual or any other dominance attribute could be discerned in bachelor groups during the present study. For instance, L<sub>6</sub> was recorded as leading the core group of which he was a member, although theoretically he should have been the lowest-ranking individual in the social hierarchy. This contrasted strongly with the position in Burchell's zebra where Klingel (1967) described an adult stallion as being the leader in bachelor herds. However, he could not distinguish social hierarchies among the adult stallions in bachelor herds and never observed a fight for social position in bachelor herds. As Joubert (1972) aptly stated: "An amicable atmosphere is present within the bachelor unit".

#### *Attachment between bachelor groups and breeding herds*

Bachelor groups often attach themselves to a breeding herd and remain with the herd for varying lengths of time. It seems likely that in such a bachelor group at least one of the bachelors originated in the herd to which the group is attached. This was observed on a number of occasions where the origin of the bachelors was known. This may have been merely coincidental. Even if proven to be the case, it may be a product of an artificially crowded population in a restricted area. In the pre-park era, herds could roam the mountain ranges and the bachelor groups in particular would probably have ranged far. This would have made contact with the parental herd less likely.

Joubert (1972) studying a Hartmann zebra population confined to an enclosure of 1 100 ha also reported attachment of bachelor groups to breeding herds, whereas Klingel (1967) studying a free-ranging Burchell's zebra population, did not. This difference in behaviour could therefore be a species attribute, but as the social organisation of the two species is virtually identical, a more plausible explanation would be that it is a result of confinement to a limited area.

The close association of a group of bachelors with a breeding herd could be detrimental, as the following example will illustrate: Grootkloof, the easternmost kloof of the MZNP is rather isolated from the plateau to the west. The kloof was inhabited by two breeding herds, which occasionally ranged beyond it. A small group of bachelors also occurred in the kloof in 1967, consisting of bachelors originating from the herds in the kloof. By

1971 the stallion of one of the herds had disappeared and been replaced by one of the bachelors who had originated in that herd. His mother was still one of the mares in the herd. This inbreeding could be detrimental and may be the product of the artificial confinement of the population to a limited area. Such an occurrence would have been improbable under natural conditions.

*Aspects of the possible evolution of the social structure in E. zebra*

In the summary of the social behaviour of African Equidae, Klingel (1972) described two distinct types of social organisation. In *E. zebra* and *E. burchelli* non-territorial breeding herds (with social hierarchies) of one adult stallion, various mares and their offspring exist, while *E. grevyi* and *E. asinus* are territorial with no permanent bonds between two or more adult animals. In *E. grevyi* this behaviour was described in detail by Klingel (1969c). *Equus caballus* (Bruemmer 1967; Feist 1971; Tyler 1972) and *E. przewalskii* (Bannikov 1958, In: Fisler 1969) have a social organisation similar to *E. zebra* and *E. burchelli*. The social organisation of *E. hemionus* has not yet been reported in detail, although Klingel (1974) stated that it may be similar to *E. zebra*, *E. caballus* and *E. burchelli*.

Fisler (1969) stated that hierarchy and territory are different ways of solving adjustment of populations to their environment, both abiotic and biotic, but having the same base (site attachment and aggression), should be considered as opposite extremes of a continuum of organisational systems of mammals. Geist (1974) demonstrated that both territorial and hierarchial systems are equally ancient and that there is little reason to believe that the hierarchial social system as such evolved from the territorial one, or *vice versa*.

Eisenberg (1965) stated that morphologically primitive mammal species are generally small, forest-inhabiting forms and that these two attributes do not favour the formation of complex groups. According to Simpson (1951) *Hyracotherium*, a probable ancestor of recent equids, was a small, browsing, bush-dwelling animal. Evidence has been presented that at least some of the recent small antelopes, which tend to be bush-inhabiting browsers, are territorial. Dik-dik *Madoqua kirki* were shown to be territorial by Tinley (1969) and Hendrichs & Hendrichs (1971). Hendrichs (1972) stated that klipspringer, grey duiker, steenbok and bushbuck *Tragelaphus scriptus* are probably all territorial. Heinichen (1972) reported evidence suggesting that red duiker *Cephalophus natalensis* and suni *Nesotragus moschatus* may be territorial. Walther (1968) reported territoriality in Maxwell's duiker *C. maxwelli* and klipspringer and suspected it in all the dik-diks *Madoqua* species. Jarman (1974) stated that all the duikers, dik-diks and Neotraginae (except oribi *Ourebia ourebi*) that have been studied closely have been found to be territorial. "Scent marking is important in territorial marking, defaecation on regularly used dung heaps being particularly no-

ticeable. The importance of scent marking of territory is increased by the absence of other forms of display. Possession of territory is not advertised by calls nor by long-distance visual displays, either of which would be incompatible with these species' anti-predator behaviour which depends upon inconspicuousness" (Jarman 1974). Klingel (1972) suggested that the behaviour of *Hyracotherium* may well have been similar to that of the recent small antelopes. However, Walther (*in litt.*) warned against over-simplification in this regard. He pointed out that there have been no detailed studies of free-ranging forest duikers *Cephalophus* spp. and their supposed territoriality is an assumption. Furthermore, most Cervidae are forest-inhabiting, yet most are not territorial. The single cervid where territoriality is evident beyond any doubt is the roe deer *Capreolus capreolus*.

Klingel (1972) stated that a further probable indicator of territoriality in primitive equids is the concavity in the nasals in front of the eyes which may indicate the presence of pre-orbital scent glands, as in many recent antelopes (Simpson 1951). If present, these scent glands may have been used for marking territories, a situation analogous to that in some recent antelopes. However, Walther (*in litt.*) also warned against generalisation here. He pointed out that some territorial gazelles e.g. dorcas gazelle *Gazella dorcas* and Grant's gazelle *G. granti* have pre-orbital glands, but do not use them for marking their territories. In Cervidae, most species have pre-orbital glands and do mark, but are not territorial.

Territoriality in primitive equids is assumed here, for circumstantial evidence from various angles seems to suggest it, but it should be borne in mind that it remains a hypothesis.

Fisler (1969) pointed out that there is a general size increase from the smaller species holding spatial territories to the larger species holding other systems. According to Eisenberg (1965), specialisation in almost all eutherian orders involved an increase in size with a corresponding increase in mobility, which was often accompanied by specialisation for diurnality. These characters favour the formation of social groups. There also was a trend towards the evolution of larger brains and more complex sense organs, which made possible the formation of complex, cohesive social organisations. In the Equidae, the increase in size and brain capacity was accompanied by an adaptation to grazing, hence forsaking the forested areas and inhabiting the grasslands (Simpson 1951). Ewer (1968) pointed out that for large grazing mammals living in open terrain and depending for safety on swift flight, there are advantages in being gregarious, e.g. through group vigilance and group defence.

The primary function of a territory is to ensure an area with sufficient food and shelter for the holder, but even here there is some selection of males (Ewer 1968). In recent ungulates, territoriality has become a system for ordering reproductive competition among males (Owen-Smith 1972). If herds are formed, inter-male competition for females is likely to occur which will lead to selection for male intolerance. Simultaneously there will be a strong selection for avoiding lethal contest between males.

A harem-type organisation with each territorial male maintaining a

number of females on his territory, as in certain antelopes and the vicuna *Vicugna vicugna* (Koford 1957), would meet the requirements of both male selection and the advantages of being gregarious in open terrain. This probably represented the social organisation of early open plains-dwelling equids from which the two distinct types of social organisation in recent equids may have evolved.

Where a harem-type system is in operation, the territory as such may eventually lose its importance and the male, instead of defending a specific area, simply defends his group of females (Ewer 1968). The latter seems to have been the case in *E. zebra* and *E. burchelli*. This is what Fisler (1969) termed a "shifting arena defensarium".

The advantages of not being tied to a specific area while still retaining a permanent group of mares are obvious. It allows the animals to move around freely in search of the best grazing conditions, while the stallion is constantly in attendance at his herd and can prevent mating between his mares and any other stallion.

In the absence of harem groups, as in *E. grevyi* and *E. asinus* (Klingel 1972) and white rhinoceros *Ceratotherium simum* (Owen-Smith 1972), the territorial male tolerates other males in his territory as long as they remain submissive.

The system in *E. grevyi* (Klingel 1969c) where the mares and non-territorial stallions emigrate during the dry season while the territorial stallions remain on their territories, at first seems anomalous, as the mares and non-territorial stallions would be together for a certain period each year and mating could take place. If, however, oestrus is linked to rainfall, as seems probable, successful mating will only take place when the mares are back with the territorial stallions during the rainy season. Klingel described an oestrus mare outside a territory, with nine stallions in attendance. No stallion succeeded in mating, due to the interference by the others. Once inside a territory, however, she was soon mated by the territorial stallion.

Thenius (1966) regarded the zebras as being the most specialised equids. Heinichen (1970) reached the same conclusion on the basis of karyological evidence. If *E. caballus*, *E. przewalskii*, *E. burchelli* and *E. zebra* were more closely related to each other than to the other equids, it would be tempting to speculate that their behaviour was derived from that of *E. grevyi* and *E. asinus*. If *E. caballus* and *E. przewalskii* on the one hand and *E. burchelli* and *E. zebra* on the other were not closely related, as could possibly be implied by their chromosome numbers (Table 8), the two types of social organisation described in recent equids would represent an example of parallel evolution. The harem-type non-territoriality in *E. caballus* and *E. przewalskii* on the one hand and *E. burchelli* and *E. zebra* on the other would then have evolved independently.

The similarity of the social organisation of *E.z. zebra*, *E.z. hartmannae* and the various races of *E. burchelli* living under a wide spectrum of environmental conditions probably implies that this type of organisation has a wide ecological tolerance range. Crook (1970) stated that social structure is a "dynamic system expressing the interactions of a number of factors

Table 8

*Chromosome numbers (2n) of Equus species, after Heinichen (1970)*

Species	Chromosomes
<i>E. przewalskii</i>	66
<i>E. caballus</i>	64
<i>E. asinus</i>	62
<i>E. hemionus</i>	56
<i>E. grevyi</i>	46
<i>E. burchelli</i>	44
<i>E. zebra</i>	32

within both the ecological and social milieux that influence the spatial dispersion and grouping tendencies of populations within a range of lability allowed by the behavioural tolerance of the 'species'. The two factors which Crook & Goss-Custard regarded as particularly important determinants of social structure were predation and the abundance and dispersion of a population's resources. Eisenberg (1965) regarded social organisation as potentially the most variable structure characterising a given species, as it reflected the sum total of all the adjustments to the environment in terms of habitat exploitation and energy budget.

Some recent studies have shown that the social organisation within species may differ according to the habitat, e.g. the Uganda kob *Kobus kob thomasi* (Leuthold 1966), blue wildebeest *Connochaetes taurinus* (Estes 1969) and certain primates (Struhsaker 1967a, 1967b; Crook & Goss-Custard 1972; Eisenberg, Muckenhirn & Rudran 1972). This emphasises the importance of studying different subspecies or races of the same species for comparative purposes.

#### *Acknowledgements*

My sincere thanks are due to the National Parks Board of Trustees for permission to use the results of this study for a dissertation; to my supervisor, Prof. J. du P. Bothma, and my co-supervisor, Dr. G. de Graaff; to Dr. Hans Klingel; to Mr. and Mrs P. F. van Straaten, Mr. and Mrs W. J. Prinsloo and Mr. and Mrs. P. J. L. Bronkhorst; to Messrs April Butoman, Petrus Danster and Mayedwa Kilani; to Mr. A. Bannister; to Robert and Dorothy Seyfarth; to Dr. E. Vrba; to Dr. G. K. Theron and to Mrs M. M. Kahts.

## REFERENCES

- ACOCKS, J. P. H. 1975. Veld Types of South Africa. 2nd Ed. *Mem. bot. Surv. S. Afr.* 40:1-128.
- ANSELL, W. F. H. 1971. Order Artiodactyla. In: MEESTER, J. and H. W. SETZER (Eds) *The mammals of Africa: an identification manual*. Washington, D.C.: Smithsonian Institution.
- BRUEMMER, F. 1967. The wild horses of Sable Island. *Animals* 10: 14-17.
- COOLEY, M. W. and P. R. LOHNES. 1971. *Multivariate data analysis*. New York: John Wiley.
- CROOK, J. H. 1970. Sources of cooperation in animals and man. *Soc. Sci. Inform.* 9:27-48.
- CROOK, J. H. and J. D. GOSS-CUSTARD. 1972. Social ethology. *A. Rev. Psychol.* 23: 277-312.
- DE GRAAFF, G. and J. A. J. NEL. 1970. Notes on the smaller mammals of the Eastern Cape National Parks. *Koedoe* 13: 147-149.
- DE VORE, I. 1965. *Primate behaviour: field studies of monkeys and apes*. New York: Holt, Rinehart and Winston.
- EIBL-EIBESFELDT, I. 1970. *Ethology: the biology of behaviour*. New York: Holt, Rinehart and Winston.
- EISENBERG, J. F. 1965. The social organisation of mammals. *Handb. Zool.* 10(7): 1-92.
- EISENBERG, J. F., N. A. MUCKENHIRN and R. RUDRAN. 1972. The relation between ecology and social structure in primates. *Science, N.Y.* 176: 863-873.
- ESTES, R. D. 1969. Territorial behaviour of the wildebeest (*Connochaetes taurinus* Burchell, 1823). *Z. Tierpsychol.* 26: 284-370.
- EWER, R. F. 1968. *Ethology of mammals*. London: Logos Press.
- FEIST, J. D. 1971. Behaviour of feral horses in the Pryor Mountain Wild Horse Range. Master's thesis, Univ. of Michigan.
- FISLER, G. B. 1969. Mammalian organizational systems. *Contr. Sci.* 167:1-32.
- GEIST, V. 1974. On the relationship of social evolution and ecology in ungulates. *Am. Zool.* 14:205-220.
- GITTINS, R. 1969. The application of ordination techniques. *Br. ecol. Soc. Symp.* 9:37-66.
- HEINICHEN, I.G. 1970. Karyological studies on southern African Perissodactyla. *Koedoe* 13:31-108.
- HEINICHEN, I. G. 1972. Preliminary notes on the suni, *Nesotragus moschatus*, and the red duiker, *Cephalophus natalensis*. *Zool. afr.* 7:157-165.
- HENDRICHS, H. 1972. Beobachtungen und Untersuchungen zur Ökologie, insbesondere zur sozialen Organisation, ostafrikanischer Säugetiere. *Z. Tierpsychol.* 30:146-189.
- HENDRICHS, H. and U. HENDRICHS. 1971. *Dikdik und Elefanten*. Munich: R. Piper Verlag.



- JARMAN, P. J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour* 48: 215–267.
- JOUBERT, E. 1972. The social organisation and associated behaviour in the Hartmann zebra *Equus zebra hartmannae*. *Madoqua Ser. 1* 6: 17–56.
- KLINGEL, H. 1967. Soziale Organisation und Verhalten freilebender Steppenzebras. *Z. Tierpsychol.* 24: 580–624.
- KLINGEL, H. 1968. Soziale Organisation und Verhaltensweisen von Hartmann- und Bergzebras (*Equus zebra hartmannae* und *E. z. zebra*). *Z. Tierpsychol.* 25: 76–88.
- KLINGEL, H. 1969a. Dauerhafte Sozialverbände beim Bergzebra. *Z. Tierpsychol.* 26: 965–966.
- KLINGEL, H. 1969b. Reproduction in the plains zebra *Equus burchelli boehmi*: behaviour and ecological factors. *J. Reprod. Fert., Suppl.* 6: 339–345.
- KLINGEL, H. 1969c. Zur Soziologie des Grèvy-zebras. *Zool. Anz. Suppl.* 33:311–316.
- KLINGEL, H. 1972. Social behaviour of African Equidae. *Zool. afr.* 7: 175–185.
- KLINGEL, H. 1974. A comparison of the social behaviour of the Equidae. In: GEIST V. and F. WALTHER (Eds) The behaviour of ungulates and its relation to management. *IUCN Publ. NS* 24: 124–132.
- KOFORD, C. B. 1957. The vicuna and the puma. *Ecol. Monogr.* 27: 153–219.
- KRUUK, H. 1972. *The spotted hyena: a study of predation and social behaviour*. Chicago: Univ. Chicago Press.
- LEUTHOLD, W. 1966. Variations in territorial behaviour of Uganda kob *Adenota kob thomasi* (Neumann 1896). *Behaviour* 27: 214–257.
- MARAIS, F. J. 1974. The behaviour and population dynamics of a confined colony of striped mice (*Rhabdomys pumilio*). M.Sc. thesis. Univ. of Pretoria.
- NEL, J. A. J. and J. J. L. PRETORIUS. 1971. A note on the smaller mammals of the Mountain Zebra National Park. *Koedoe* 14: 99–110.
- OWEN-SMITH, N. 1972. Territoriality: the example of the white rhinoceros. *Zool. afr.* 7: 273–280.
- PENZHORN, B. L. 1970. A check-list of the flowering plants in the herbarium of the Mountain Zebra National Park. *Koedoe* 13: 131–146.
- PENZHORN, B. L. 1971. A summary of the re-introduction of ungulates into South African National Parks (to 31 December 1970). *Koedoe* 14: 145–159.
- PENZHORN, B. L. 1974. Sex and age composition and dimensions of the springbok (*Antidorcas marsupialis*) population in the Mountain Zebra National Park. *J. sth. Afr. Wildl. Mgmt Ass.* 4: 63–65.
- PENZHORN, B. L. 1977a. Toevoegings tot the blomplantlys van die Bergkwagga Nasionale Park. *Koedoe* 19: 203–204.
- PENZHORN, B. L. 1977b. Further bird records from the Bontebok and Mountain Zebra National Parks. *Koedoe* 20: 205–207.

- PENZHORN, B. L. and P. J. L. BRONKHORST. 1976. Additions to the check-list of birds of the Mountain Zebra National Park. *Koedoe* 19: 171-174.
- PETERSEN, J. C. B. 1972. An identification system for zebra (*Equus burchelli*, Gray). *E. Afr. Wildl. J.* 10: 59-63.
- SCHALLER, G. B. 1972. *The Serengeti lion*. Chicago: Univ. Chicago Press.
- SEAL, H. 1968. *Multivariate statistical analysis for biologists*. London: Methuen.
- SIMPSON, G. G. 1951. *Horses*. New York: Oxford Univ. Press.
- SKEAD, C. J. 1958. Mammals of the Uitenhage and Cradock Districts, C. P., in recent times. *Koedoe* 1: 19-59.
- SKEAD, C. J. 1965. Report on the bird-life in the Mountain Zebra National Park, Cradock, C. P., 1962-1964. *Koedoe* 8: 1-40.
- STRUHSAKER, T. T. 1967a. Behaviour of vervet monkeys (*Cercopithecus aethiops*). *Univ. Calif. Publ. Zool.* 82:1-64.
- STRUHSAKER, T. T. 1967b. Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology* 48: 891-904.
- THENIUS, E. 1966. Die Vorgeschichte der Einhufer. *Z. Säugetierk.* 31: 150-171.
- THERON, G. K. 1973. 'n Ekologiese studie van die plantegroei van die Loskopdam-natuurreservaat. D.Sc. dissertation, Univ. of Pretoria.
- TINLEY, K. L. 1969. Dikdik *Madoqua kirki* in South West Africa: notes on distribution, ecology and behaviour. *Madoqua* 1: 7-33.
- TOERIEN, D. K. 1972. Geologie van die Bergkwagga Nasionale Park. *Koedoe* 15: 77-82.
- TYLER, S. J. 1972. The behaviour and social organisation of the New Forest Ponies. *Anim. Behav. Monogr.* 5: 85-196.
- WALTHER, F. 1968. Ducker, Böckchen und Waldböcke. In: GRZIMEK, B. (Ed). *Grzimek's Tierleben*. Zürich: Kindler Verlag. Vol. 13: 342-367.