THE SOCIAL ORGANISATION AND POPULATION ECOLOGY OF THE PLAINS ZEBRA (*EQUUS QUAGGA*)

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INTRODUCTION

In spite of the fact that the plains (or Burchell's) zebra (*Equus quagga*) is one of the commonest large wild animals, few investigators have studied it and our knowledge of its biology, ecology and behaviour in the wild is limited. From 1962 to 1965 I had the opportunity of carrying out a research programme in East Africa in an attempt to solve some of the problems and later to compare my results with those of other zebra populations in southern Africa.

Plains zebra have a wide range from the Sudan to South and South West Africa and several subspecies are recognisable. All seem to conform to the same pattern of social organisation and the differences are quantitative only.

METHODS

Zebra are in some ways a difficult species to study, because there are no marked secondary sex characters and the ages of free running animals are difficult to estimate. On the other hand each invididual has a distinctive stripe pattern which allows individual recognition as do human finger prints.

An intensive study was carried out on the Ngorongoro Crater population by following the life histories of over 600 individually known animals representing about 10% of the total population. One hundred and twenty-two zebra were marked by cropping their tails and manes, and by brands and ear tags. Immobilisation was carried out originally with succinyl-choline-chloride, later with Etorphine-Reckitt (M.99), administered with a Cap-Chur gun or a cross bow (Klingel 1967 a). The cropped manes were visible for about three months only, the tails, however, were still conspicuously square after two years and provided a means of recognition even from a distance. Brands are clearly visible probably for the life time of the animal, but some of the ear tags came out due to infections.

One of the first results of following up the marked animals was the fact that zebras form groups which are remarkably stable. This made it possible to include in the study all members of a group in which only one animal was marked. These animals could be recognised from their stripe patterns and photographs of both sides, stuck on file cards, were used in the field.

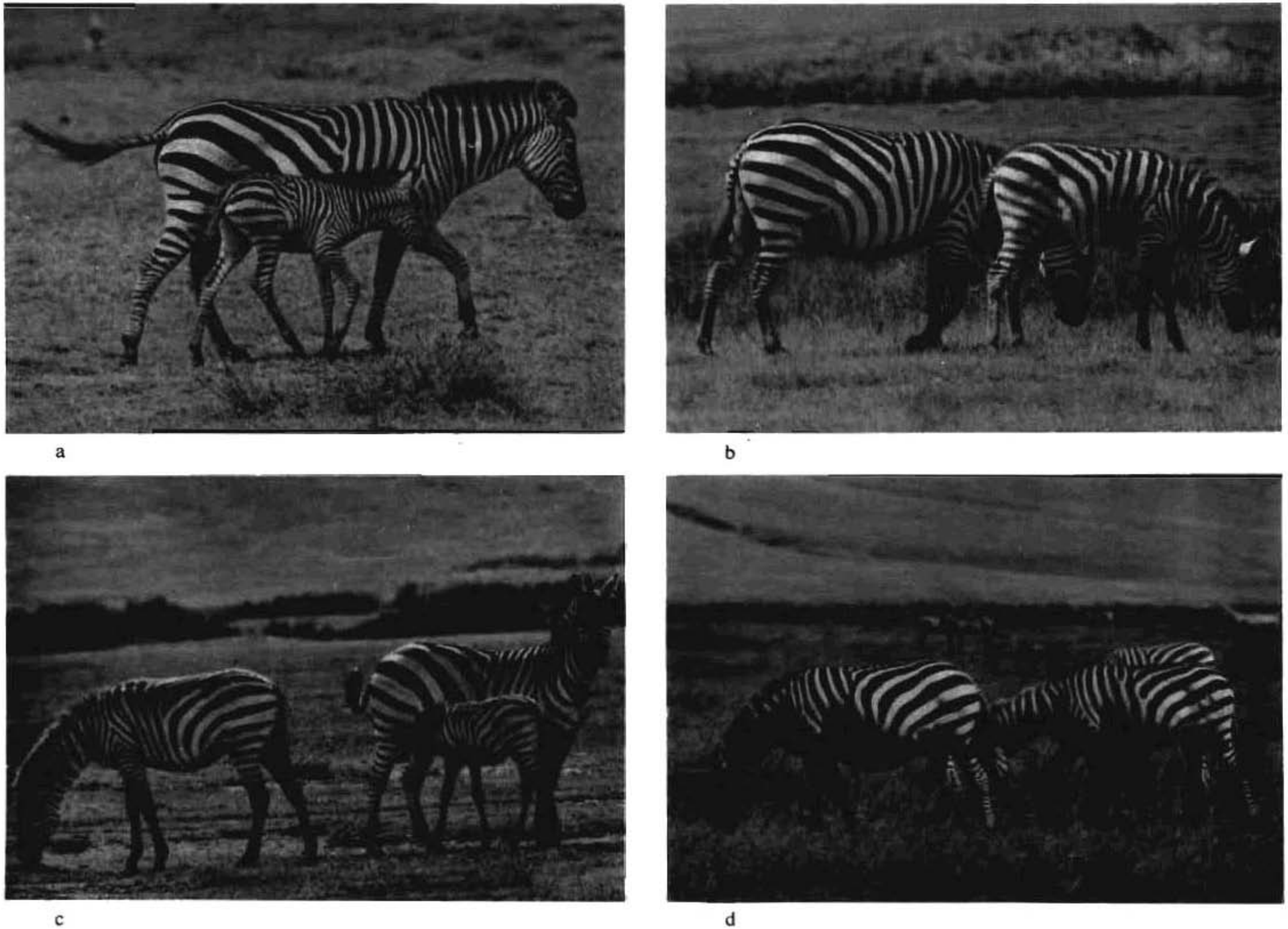

FIGURE 1
Foals of known age with their mothers which served as references for estimating the ages of other foals. (*a*) new born foal (6 hrs. old); (*b*) 6 months old; (*c*) 2 weeks and 14 months old, respectively; (*d*) 26 months old. Photographs such as these were used for the identification of individuals from their stripe patterns, in groups where one animal was marked.

TABLE 1

COMPOSITION AND SIZE OF THE GROUPS IN THE DIFFERENT POPULATIONS

Locality and date	*Family size*		*Mares per family*		*Families*	*Sample of animals in families*	*Size of stallion groups*[2]		*Groups*	*Sample*[2] *of stallions in stallion groups*	*Total sample of animals*
	Average	*Max.*	*Average*	*Max.*	*n*	*n*	*Average*	*Max.*	*n*	*n*	
Ngorongoro, Tanzania, May, 1965	7·05	16	2·8	6	60	423	2·9	9	23	270	693
Serengeti, Tanzania, March, 1965	5·1	11	2·2	5	159	810	2·7	6	46	117	927
Kruger Nat. Park, South Africa, Sept., 1965	4·5	8[1]	2·4	4	112	505	3	10	28	85	590
Etosha Pan, South West Africa, August 1965	4·7	9	2·3	5	89	415	1·6	5	40	65	480
Wankie Nat. Park, Rhodesia, Sept., 1965	4·6	8	2·6	5	102	472	2·9	6	21	61	633

[1] One group with 11 members

[2] Including solitary stallions.

Figure 2
Zebra groups in the Serengeti.

The difficulty of estimating the ages of subadult animals was overcome by using the relative sizes and proportions, compared with adults, of foals of known ages in marked groups in the Ngorongoro population. Some photographs may serve to illustrate this (Fig. 1).

For the determination of age the state of the teeth is especially suited in the zebra, as a number of conspicuous changes occur during the life time of the animal. Twenty-one different stages of tooth eruption, replacement and wear can be recognized: 7 stages with milk teeth only in various states of eruption, 4 with both milk and permanent teeth and 10 with the permanent teeth in various states of wear.

Animals of known age in the Ngorongoro population provided the aging data for up to 24 months. The age of the later stages was found by comparing the sets of teeth of marked animals that were recorded twice at intervals of 6 to 24 months, and by correlating them among themselves and with those of animals of known age. With this method an aging table could be established for the whole life time of the species (Klingel, H. and U. 1966).

SOCIAL ORGANISATION AND HOME RANGE

The organisation of the zebra society is best seen when the animals are undisturbed (Fig. 2). There are two types of groups: families, consisting of one male, one or more females and their young, and stallion groups. In addition, there are solitary stallions. The average family sizes varied considerably in the different populations analysed, from 7·1 in Ngorongoro to 4·5 in the Kruger National Park. The biggest family group ever recorded consisted of 16 members (Ngorongoro). The number of adult mares ranged from 1 to 6 and was more uniform on the average, from 2·2 in the Serengeti to 2·8 in Ngorongoro (Fig. 3 and Table 1).

As mentioned before, the zebra groups are basically stable (Table 2). Of 129 mares living in 41 family groups, 122 (95%) were still in the same groups after two years. 2·5% of the mares were thus lost from the groups per year. Their fate is not known, but most of them can be expected to represent natural loss. However, some observations indicate that mares

TABLE 2

THE MAJOR RESULTS GAINED FROM THE MARKED GROUPS

1. Families of the first series, marked in 1963. 41 families observed for two years.	
Stallions and mares unchanged	in 29 families
Stallions replaced	in 5 families (3 dead, 2 to stallion groups)
Mares disappeared (7) (one changed family)	in 6 families
Mares gained (1)	in 1 family
Young mares gained (17)	in 12 families
Young mares lost (40)	in 26 families
Young stallions lost (28)	in 22 families
2. Families of the second series, marked in 1964. 11 families observed for one year.	
Stallions and mares unchanged	in 8 families
Stallions replaced	in 2 families (to stallion groups)
Mares disappeared (2)	in 2 families
Mares gained (1)	in 1 family
Young mares gained (2)	in 2 families
Young mares lost (4)	in 4 families
Young stallions lost (4)	in 4 families
3. Stallions of the first series (1963). 12 individuals observed for two years.	
Always in stallion groups or solitary	8 stallions
Family taken over	6 stallions
Family lost again	4 stallions (of which 2 died)
4. Stallions of the second series (1964). 21 individuals observed for one year.	
Always in stallion groups or solitary	15 stallions
Family gained	7 stallions
Family lost again	4 stallions (one during immobilisation)

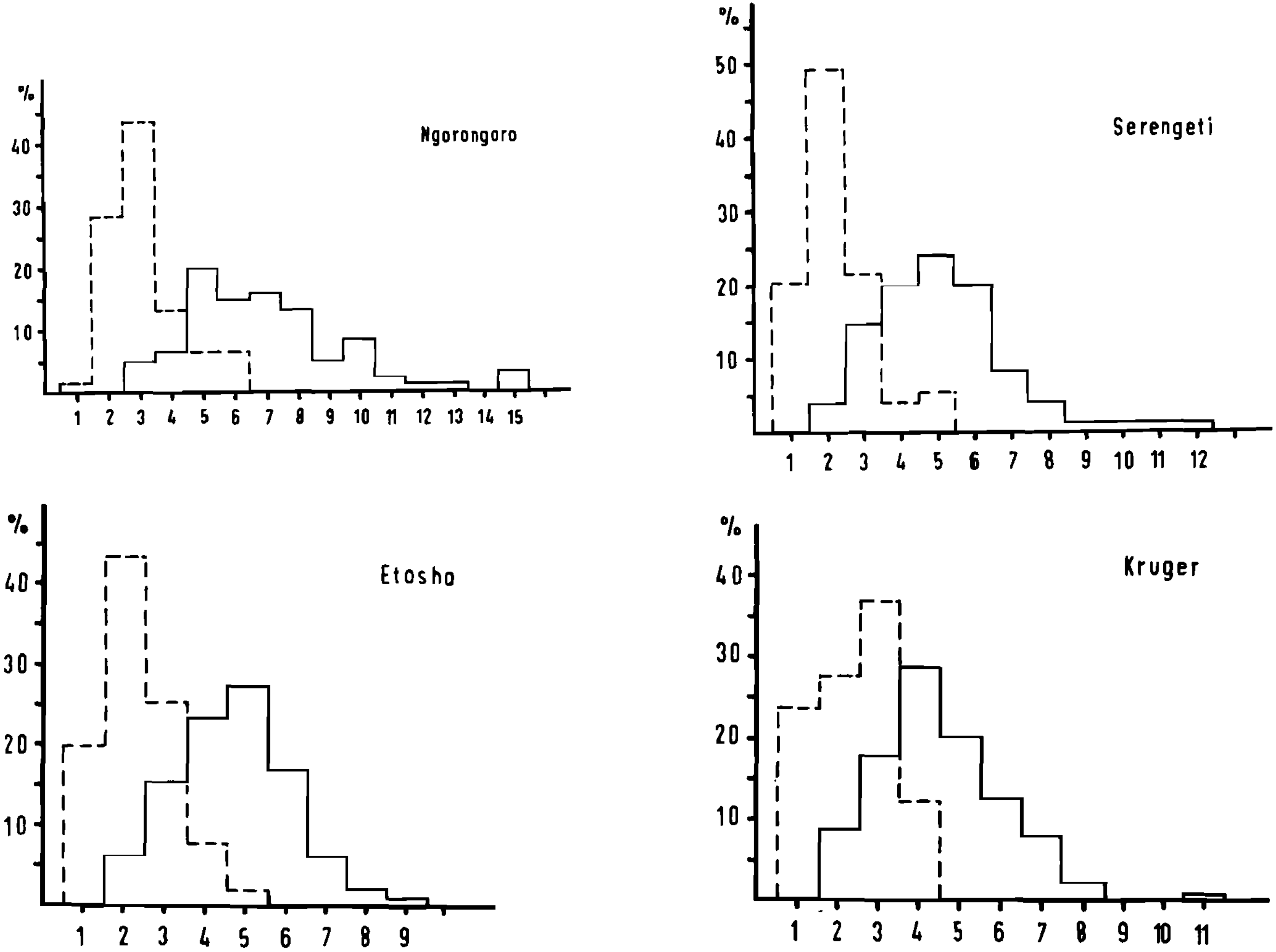

FIGURE 3
Family composition of 4 zebra populations. Solid line: total family size; dotted line: number of mares per family, both in per cent. Samples as in Table 1.

do occasionally change from one group to another, though very rarely. In one case an individually known mare had joined a new family group and was found several kms. away from her original group. She did, however, return a few days later, thus demonstrating the strong family bonds.

In 5 families the (marked) stallion was replaced by a new one. In 3 cases the original stallions disappeared and can be assumed to have died. In the 2 others they were later found in stallion groups. In all these cases and in some others caused by the death of the family stallion during the immobilisation, the other members of the families stayed together and were taken over as a whole by a new stallion. This shows, that the family groups are kept together by personal bonds between the members, and not by force executed by the stallion.

The cohesion of the families is also demonstrated by their exclusiveness. The mares do not communicate with, but are antagonistic towards members of other groups. The stallions, however, contact all other stallions in the vicinity and greet them in a set ceremony; the foals play occasionally with foals of nearby families.

Adolescent animals disappear from their family groups. The young mares are abducted by other stallions at the time of oestrus, which occurs first at the age of 13 to 15 months. Stallions in the vicinity of the group are attracted by the typical posture of the mares during this time, and also by the smell of their oestral secretions. The stallions get involved in serious fighting with the defending family stallion, but usually, because of their number, succeed in separating the young mare from her group and chasing her away. Abducting stallions, may be family stallions, who in this manner increase the number of mares in their groups or they are bachelors who start a new family.

The young stallions leave their groups at the age of 1 to about 4½ years. This process has no direct relation to their sexual maturity and there is no antagonism between them and their father or other members of the group. The timing depends on several factors:

(*a*) the young stallion's mother has a new foal and thus the bonds between them are loosened. If the foal dies, the original relationship is re-established.

(*b*) There are no other male foals of about the same age in the groups and there is thus a lack of playmates for the fighting games typical of that age group.

(*c*) There are stallion groups with such playmates nearby.

If all these factors coincide, the young stallions leave their families at the age of a little over one year. Otherwise they may stay up to about 4½ years.

After leaving their original families the young stallions join bachelor groups. These groups are more variable in their composition, but personal bonds between the members are equally evident. Many of the groups observed consisted of the same individuals for the whole time of observation. However, other stallions often joined them for short periods.

Plains zebra are not territorial, i.e., they do not mark or defend any particular areas, nor do they respect areas already occupied. They move freely in large ranges which they share with other zebras. No organisation above the level of the family and stallion groups was found to exist (for details see Klingel 1967 b).

This type of social organisation is unique in being based on non-territorial coherent families and stallion groups kept together by personal bonds between the members. A similar type of organisation exists in the mountain zebra (*E. zebra zebra* and *E. z. hartmannae*) (Klingel 1968).

Once the principles of the organisation of zebra populations had become clear, population ecology data could be collected which would have been difficult to gain otherwise. With the results of these investigations it was then possible to analyse other populations where an intensive study could not be made.

The zebra populations of the Serengeti and the Ngorongoro Crater were always, during the time of observation, split up into several herds, distributed over the area and moving according to the seasonal changes of the habitat. Each of these herds, which were by no means stable, had a common sleeping ground where they stayed for the night and certain grazing zones which they occupied during the day. This behaviour was studied in 1963/1964 in Ngorongoro by mapping the sleeping grounds in the evening and by following the daily migrations from there to the grazing areas.

At the beginning of the dry season in June, 1963, three major sleeping grounds were occupied in the vicinity of the lake. Day grazing was in the long grass areas in dry parts of the crater floor (Fig. 4a). Later in the dry season (August) the zebra used a further sleeping ground near the southern crater wall. During the day they grazed mainly on the slopes, to some extent also on the drying-up edges of the swamps. During that time they made daily migrations of up to 13 km. each way (Fig. 4b). Towards the end of the dry season (October) the population was split into 7 herds with 7 different sleeping grounds. The animals grazed almost exclusively in the dried-up swamps which still had green vegetation. The grazing areas were up to 6 km. away from the sleeping grounds (Fig. 4c). After the start of the rains (November) there was ample food all over the crater floor as well as outside the crater. Four sleeping grounds were used in the crater and 2 more outside, in Olbalbal and Malanja, the latter 2 by 1,500 animals that had emigrated from the crater (Fig. 4d). With the increasing rainfall (January, 1964) one of the sleeping grounds in the crater became inundated and was abandoned by the zebra (Fig. 4e). The grazing areas were less extensive than in November. Towards the end of the rainy season (May) the emigrants returned to the crater and the population was split into 3 herds again (Fig. 4f). Up to June, 1965 when the investigations were ended, similar changes in the distribution continued to take place. The distribution was found to be very much influenced by the conditions of the grazing areas which in turn depended on the burning patterns during the dry seasons.

The sleeping grounds were always in open, dry places, with short grass cover. Some of them were used throughout the year, others only periodically.

During the whole time of observation the positions of marked animals were mapped and thus their ranges could be determined. The results showed that the zebras used only part of the area of distribution of the whole population. All families, stallion groups and solitary stallions, have their particular home range within which they move independent of the movements of other zebra. Some examples of overlapping home ranges are given in Figure 5. Some home ranges in the South West corner of the crater were only 80 km.^{2} in size; others extended over 150 to 250 km.^{2}

In the Serengeti the ranges could not be studied in detail. However, from observations

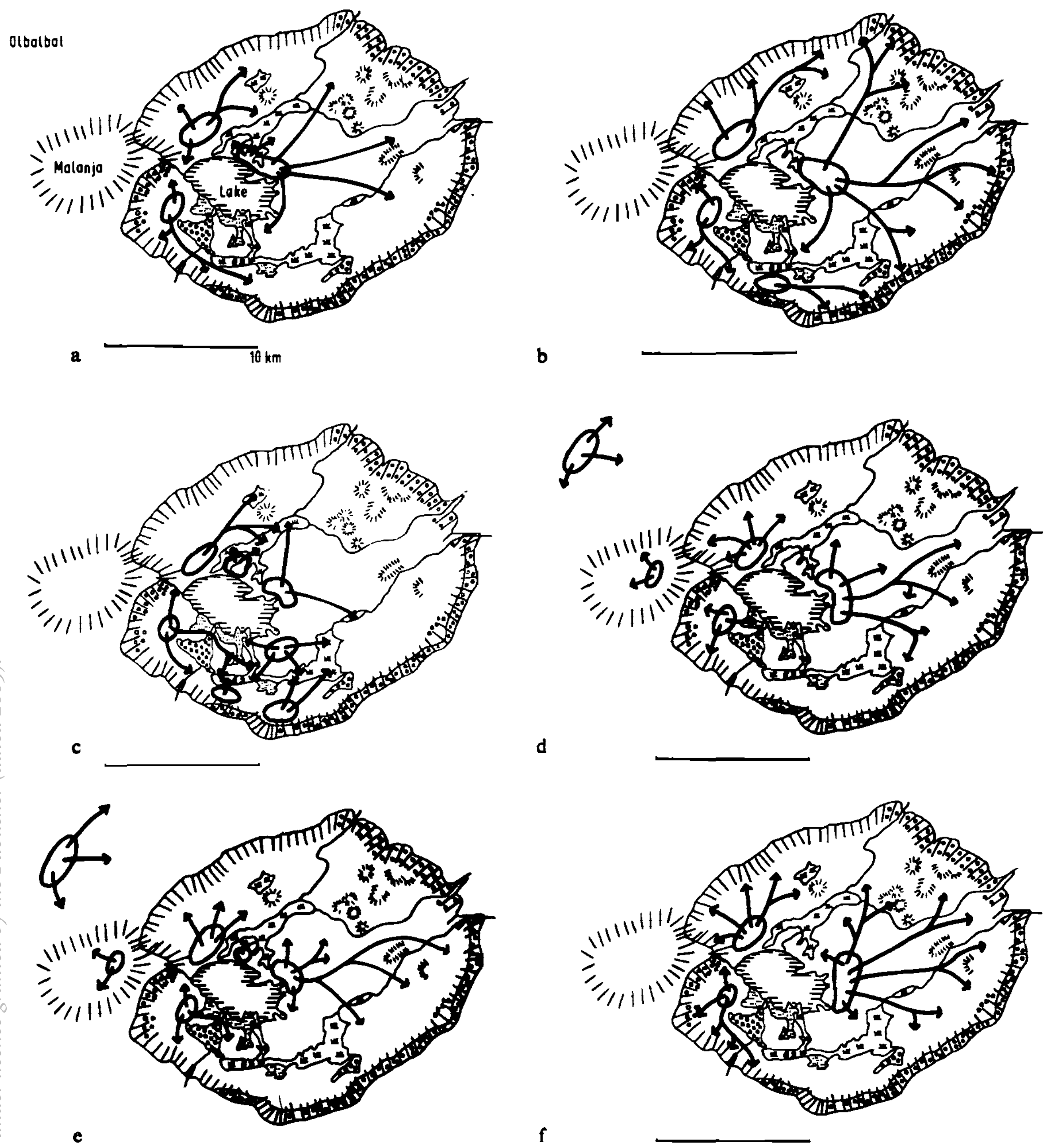

FIGURE 4
Sleeping grounds (ovals) and daily migrations to the grazing areas (arrows) of the herds of the Ngorongoro zebra population in 1963/1964. (*a*) June, 1963; (*b*) August, 1963; (*c*) October, 1963; (*d*) November, 1963; (*e*) January, 1964; (*f*) May, 1964.

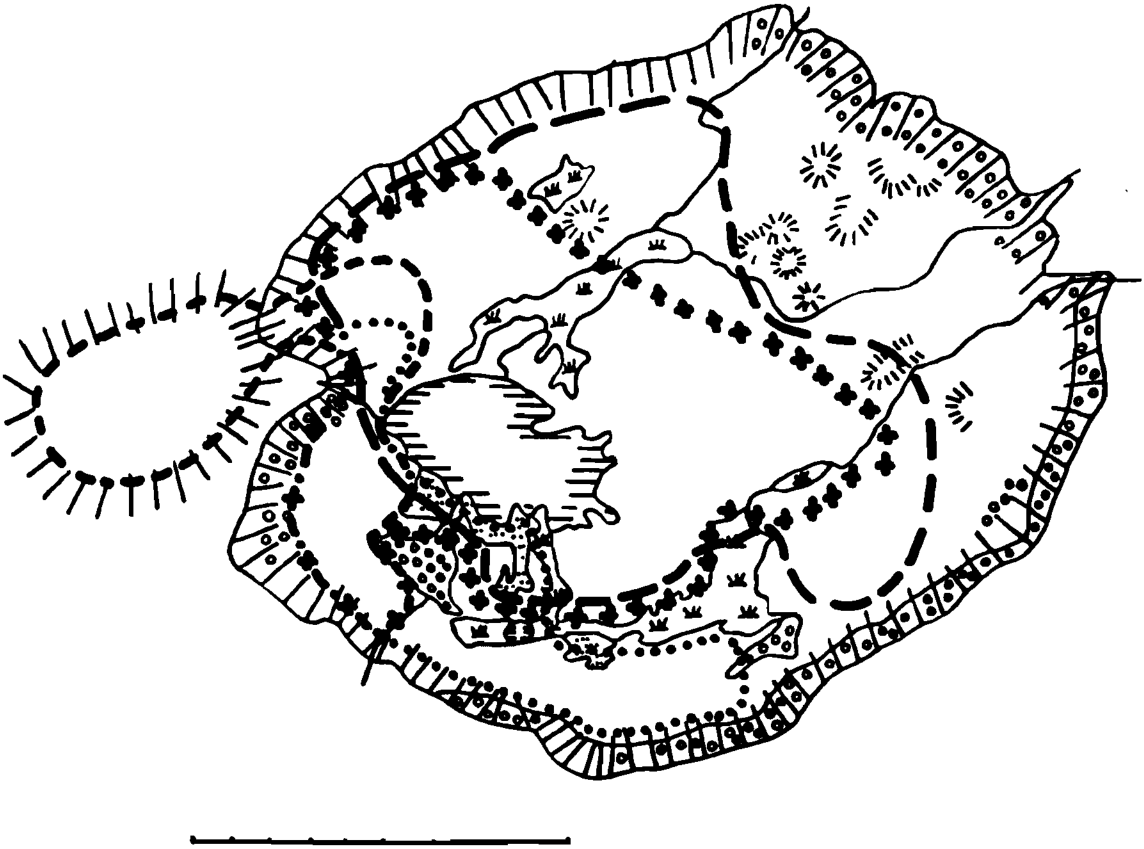

FIGURE 5
Home ranges of 4 zebra families, 1963 - 1965, in Ngorongoro Crater, selected to show the differences in size.

of the grazing and migration patterns it has become clear that individuals used areas of 3-400 km.² during the rainy season in the Serengeti plains and another 4-600 km.² in the bushland during the dry season, in addition to the migration routes which are 100 to 150 km. long (one way). The total individual ranges of the Serengeti zebra can thus be estimated to be at least 1,000 km.², but probably they are even larger. It is not yet known if the same individuals use the same areas in consecutive years; only by following marked animals will it be possible to obtain this information.

REPRODUCTION AND POPULATION DYNAMICS

Maturity is reached rather late in the plains zebra. The oldest male foal recorded in a family group was 4½ years old. This was quite unusual, but it demonstrates that even at that age the young stallion was not considered to be a competitor by his father. The youngest family stallions immobilised were found to be 5 to 6 years old. Possibly sexual maturity is reached earlier as is indicated by observations in zoological gardens. Under natural conditions, however, a stallion will not be physically and psychologically strong enough to compete with other stallions for young mares before the age of about 5 years.

Mares have their first foal at the age of 3½ years, thus they are not fertile before the age of 2½ in spite of the fact that they have their first oestrus at the age of about 13 months.

Zebra foals are born during the whole year. In the Ngorongoro population the foaling distribution could be worked out by recording the newborn foals in the marked families each month. Of 151 foals, 28% were born in January, 61% during the main foaling season from January to March, 85·5% during the 6 months from October to March and only 14·5% during the rest of the year. This distribution is linked with the rainfall (Fig. 6a): most of the foals (over 80%) are born during the rainy season. The curves are based on the actually recorded foals, of which some may have been up to 2 weeks old. Thus the post-natal mortality could not be assessed. There was, in this population, practically no loss of foals: of 158 observed for at least one year, only 8 (5%) disappeared.

With the progress of the foaling season the percentage of adult mares with a foal of the season increased and a maximum of 50·5% was reached in June (1964). The value dropped to 48·1% in October, disregarding the foals of the new season (Fig. 7).

In the Serengeti it was not possible to follow up individual groups as the population consisted of 150,000 animals which were distributed over an area of 20,000 km.^{2} For this reason the percentage of mares with a foal of the season was recorded at monthly intervals and from these results the monthly increase, i.e., the foaling distribution, could be calculated. Here again, post-natal mortality could not be assessed. A total of 2,873 mares and 705 foals were recorded at monthly intervals. The increase of mares with a foal was quite marked from October (2·3%) to March (44·0%). The maximum was reached in April with 45·0%. The values then remained constant through May, i.e., the number of foals born equalled mortality. In October the values dropped to 31·4% (Fig. 7 dotted line). The mortality of foals from May to October was thus 30% in addition to the post-natal mortality.

From these figures the seasonal distribution of foaling reaches a maximum of 25·1% in January. 66·3% of the foals are born during the main foaling season from December to February, 95·0% during the 6 months from October to April and only 5% during the rest of the year. By using the method described, only the differences between birth rates and mortality can be assessed.

In the other populations analysed, in Etosha Pan, Kruger and Wankie National Parks, the age composition of the foals of up to one year showed a similar correlation of the foaling with the rainfall distribution.

Potentially the plains zebra have a reproductive rate of one foal per year. Mares come into heat a few days after having given birth to a foal. Gestation length is known from zoological gardens to be about one year (Wackernagel 1964). The shortest intervals recorded in freeliving animals in the Ngorongoro population were 378 and 385 days. Out of 120 adult mares that were followed up for three foaling seasons, 18 (15%) had 3 foals, i.e., one each

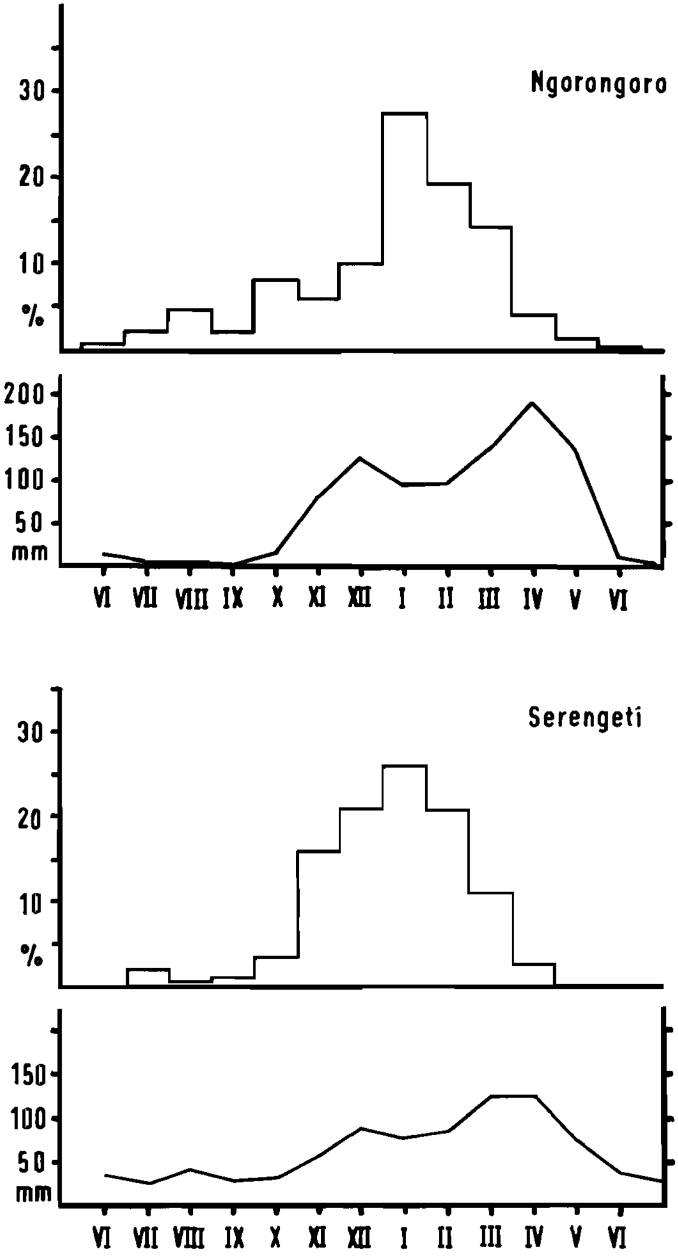

FIGURE 6
Foaling seasons (*a*) in Ngorongoro and (*b*) in the Serengeti, and rainfall distribution.

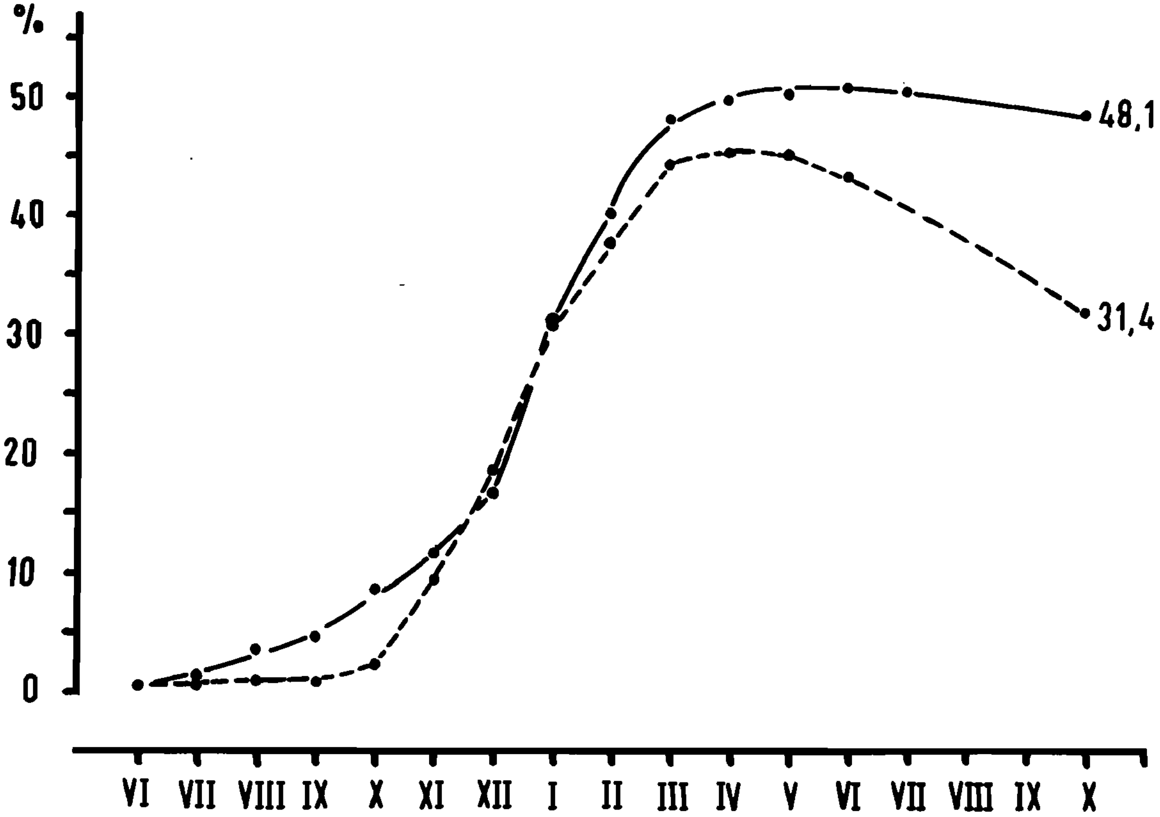

FIGURE 7
Percentages of mares with a foal of the season in the Serengeti (dotted line) and Ngorongoro (solid line).

season, 40 (33%) had 2 foals, 50 (41%) had one and 12 (10%) had no foal at all. These figures again are based on surviving foals.

For the study of populations, the actual birth rate is of little value, especially since it will be influenced considerably by irregular conditions. Furthermore, it could only be assessed by shooting a large sample of mares.

For several reasons the recruitment rate of adults into the population cannot be calculated. Firstly, because of the late maturity (see below) of the plains zebra and the difficulty of estimating the ages of subadults. Secondly, because of the changing over of the subadults from their original families to other groups, the timing of which has been found to be influenced by the population density and occurs earlier in larger concentrations. Thirdly, because of a certain amount of segregation of stallion groups and families.

The number of foals per 100 mares, however, is a value relevant to recruitment and it was interesting to compare the results of different populations, especially in relation to the rainfall figures.

In Ngorongoro the percentage of mares with a foal of the previous season was 48·1 at the beginning of the next season (October, 1964). In the Serengeti it was 31·4% (October, 1965). The figures for the other populations were obtained some time before the beginning of the next season. By then, there would have been further mortality. They were 26·8% in the Kruger National Park (September, 1965), 14·5% in Wankie (September, 1965) and 13·8% in Etosha (August, 1965). This order is also the order of the rainfall figures: Ngorongoro: 907·5 mm.; Serengeti: 772·6 mm.; Kruger National Park: 616·7 mm.; Wankie: 590 mm.; Etosha: 323 mm. per year. (The rainfall figures for the year of observation and for the previous year seem to be more important to birth and survival rates than average rainfall. Other factors, e.g. burning, population density and predator pressure should also be considered.)

Easier to determine is the number of foals plus subadults in the families per 100 mares, as it is then unnecessary to estimate the ages. These figures also give an indication of the recruitment rate. Because of the reasons mentioned above they are, however, not fully comparable. They ranged from 129% (i.e., 129 foals plus subadults per 100 mares in the families) in the Ngorongoro population to 49% in the Kruger population.

The very high recruitment in the Ngorongoro and Serengeti populations is attributed to the fact that the years previous to the study were extremely dry and probably caused a decline in the original population numbers.

SUMMARY

1. Plains zebra are organised in non-territorial coherent families and stallion groups. The families consist of one male, one or more females and their young. Adolescent foals leave their families at the age of 1 to 4½ years.

2. The populations of Ngorongoro and Serengeti are subdivided into a varying number of herds which congregate in suitable sleeping grounds and grazing areas.

3. The home ranges of individuals were found to extend over only a part of the area of distribution of the population.

4. Maturity is reached at 5 to 6 years in stallions and at 2½ years in mares.

5. The foaling distribution is correlated with the distribution of rainfall and has a peak during the rainy season.

6. In Ngorongoro 50% of the mares had a surviving foal per year during 1963 to 1965. In other populations this percentage was smaller. Productivity is correlated with rainfall.

ACKNOWLEDGMENTS

The research work in East Africa was financed by F.A.O., the Fritz Thyssen Stiftung and the Michael Grzimek Stiftung, and supported by Tanzania National Parks and the Ngorongoro Conservation Unit. The study of the zebra populations in southern Africa was made possible by a grant from the Fritz Thyssen Stiftung. I gratefully acknowledge the assistance received by the National Parks organisations of South Africa, South West Africa and Rhodesia. Special thanks are due to my wife for her assistance.

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