

## **Density, distribution, population structure and social organization of the black rhinoceros in Masai Mara Game Reserve**

JOHN G. MUKINYA *Kenya Game Department, Research Division, P.O. Box 40241, Nairobi and Department of Zoology, University of Nairobi*

### **Summary**

Black rhinoceros were studied in the Masai Mara Game Reserve from May 1971 to August 1972. Data were gathered on their density, distribution, population structure, social organization, feeding habits and daily activities.

The study area, its vegetation, and the study methods are described briefly. Rhino occupied thirteen separate distribution areas, their distribution being influenced by food availability, water, cover and the presence of human and domestic animals. The number of rhino in each distribution area were within the range of one to thirty-one (densities 0.04 to 0.24/km<sup>2</sup>), giving a mean density in the rhino-occupied area (749 km<sup>2</sup>) of 0.14/km<sup>2</sup> and in the whole study area (1530 km<sup>2</sup>) of 0.07/km<sup>2</sup>.

Of the 108 rhino in the population, 73% were adult and 27% were immature. At least one adult and one immature were found in nearly all distribution areas. Adult rhinos formed one age class while the immatures were divided into three age classes. Sex ratio and mortality were investigated.

Social units and their home range sizes in relation to density and distribution are discussed. Some aspects of social organization, feeding habits and daily activities will be discussed in a later paper.

In conclusion, recommendations for rhino management based on preservation of habitat, particularly cover, more sources of water and human settlement are discussed. Suggestions for further lines of research are also discussed.

### **Introduction**

In Africa, in general, for the past few years, the slaughter of rhinoceros has been extensive, raising the question of its future status on the continent.

In the study area, in the past, some ecological work was carried out by Darling (1960); and Talbot & Talbot (1963). Some population information also appears in the writings of Stewart & Talbot (1962) and Stewart & Zaphiro (1963). In 1971 the Kenya Game Department initiated a research project on the rhino population in Mara, its distribution, population structure, social organization, feeding habits and daily activities. A vegetation survey of the study area was in progress at the same time.

**Methods**

A total of over 4000 hours were spent in the reserve during the entire study period. Patrolling was not carried out according to any rigid systematic pattern but as rhinoceros reports and evidence of rhinoceros activity dictated. At least one rhino was sighted each day.

**(a) Animal census and individual identification**

A direct count of all rhinoceros in Mara was carried out. When a rhinoceros was first encountered its location, date located and sex were recorded. In addition, as an aid to identification, a photograph of full frontal and lateral parts of each rhinoceros was taken. The frontal photograph provided valuable information for identifying rhinos by use of wrinkles between the base of anterior horn and the tip of the upper lip (Fig. 1). Other features such as shape and length of horns; hair tufts, tears and notches in the ears; and sores and scars were also used in identification.

**(b) Sex**

The two sexes could be readily distinguished by the external genitalia. It was also assumed that a rhino frequently accompanied by a juvenile was a female. It was found



**Fig. 1.** Female number 50, showing wrinkles on nose and cut on ear; features used to identify this animal.

difficult to sex juveniles less than half the mother's shoulder height because external sex organs were not clearly visible.

(c) *Age*

Conventional methods for ageing rhinos involving examination of dead specimens (Goddard, 1970) could not be used. Instead it was decided to use four individuals from the Mara rhino population whose date of birth was known. Their pictures were taken and their body size compared with the full grown individuals. This method, similar to Schenkel & Schenkel's (1969) age criteria by body growth, was most useful for rhinos which accompanied their mothers, and those which had just left their mothers. Mature rhinos whose horn growth was similar in length and shape to those rhinos which had young ones were considered to be over 4 years. This was based on Goddard's (1970) and Schenkel & Schenkel's (1969) information that rhinos attain sexual maturity at age from 5 to 6 years and full growth at age from 8 to 10 years.

Using this method, rhinos were classified into four age groups. Group I whose age was under 1 year, Group II whose age was over 1 year but under 2 years, Group III whose age was over 2 years but under 4 years and Group IV whose age was over 4 years.

(d) *Food availability*

A survey of plant species eaten by rhinos was first made in areas occupied by rhinos. Later, in February 1972 when most plant regeneration after burning was observed, herbs, trees and shrubs were sampled using a Point-Centred Quarter method, Curtis (1962). The aim was to get data for calculating relative frequency of each species. In each area occupied by rhino two transects, one in open grassland and the other in wooded grassland, were run.

(e) *Horizontal density of vegetation*

To determine the horizontal density of vegetation in various areas occupied by rhinos in the study area a cover 'density board' (Wight, 1938) was used. A series of readings gave some measure of the density of the cover.

(f) *Home range and distribution area*

The technique used in mapping home ranges was by checking the movement and locality of rhinos. I acquainted myself with points on the ground which were readily identifiable on a 1 : 50 000 map showing features such as roads, hills, waterholes and rivers. The location of rhinos on the ground was approximated on this map and then transferred to a working map of the same scale with 1 km<sup>2</sup> grids. For field use each side of 1 km<sup>2</sup> grid was divided into ten parts (each 2 mm) which were used in approximating the location. The size of home range for each animal was calculated by computing the area of a polygon which resulted from connecting the peripheral points of location.

In this paper 'distribution area' means the total area which is occupied by a group of rhinos whose home ranges overlapped but was separated by unoccupied country from other such groups of rhino.

Rhinos are solitary and their movements are confined within their home ranges. Observations revealed that there are areas in the study area which were not occupied by rhinos. Distribution areas (areas occupied by rhinos with overlapping home ranges) were lettered alphabetically and used in this paper as such.

## Study area

### (a) General description

Masai Mara Game Reserve, the study area, is in Narok District within Rift Valley Province of Kenya. It lies approximately between  $34^{\circ} 45'$  and  $35^{\circ} 25'$  East of Greenwich and  $1^{\circ} 13'$  and  $1^{\circ} 45'$  South of the Equator. The south-west extremity of the study area is adjacent to the international boundary with Tanzania (Fig. 2). The Reserve has an area of  $1530 \text{ km}^2$  (600 sq. miles).

The altitude varies from 1530 m (5000 ft) to 1900 m (approx. 6200 ft) above sea level. It is a part of the eastern catchment area of Lake Victoria.

The rainfall varies from 980 mm (30 in) per annum on the Central plains area to 1680 mm per annum on the eastern hills and the western area of Game Reserve. Rain occurs in two seasons (but is rather continuous), namely March–May and December–January.

Drainage lines to the Mara river flow mainly from east to west through the plains, the principal tributary being the Talek which is joined by the Jagartek from the north east, 6·4 km above the confluence with the Mara river. The Sand river is a considerable watercourse coming out of the Siana and Loita hills.

The streams flowing from the Siria Escarpment, the western boundary of the area, to the Mara river are short and not persistent. They appear as shallow dry stream beds or gullies or mere depressions where a certain amount of water may lie in pools or wallows puddled in the soil.

### (b) The habitat

The study area is dominated by the plains, the undulating, flat or slightly convex areas of grassland which may be some thousands of hectares in extent and often appearing as if paddocked by the narrow bands of shrubby vegetation and occasional trees which mark the dry streams. The plains may present large, unbroken areas of grassland, with occasionally a single tree.

*Plains habitat.* Plains habitat covers Meta, Mosee, Burrungali and Lorogot plains. This is medium height grassland of 0·6–1·5 m (2–5 ft). It has horizontal density cover ranging from 5·0% to 25·0% and according to Wight's (1938) classification of cover by obstruction to vision it falls under 'scarce'. The dominant plant species are *Themeda triandra* Forsk, *Setaria sphacelata* (Schumach), *Pennisetum meyanum* (Leeke), *Solanum incanum* Linn., stands of *Acacia hockii* De Wild and *Acacia drepanolobium* Sjoestedt. Also on the plains particularly lowland grassland there are *Dichrostachys cinerea* (L.) Wight and Arn., *Becium* species and *Commelina* species.

The thickets are mainly dominated by *Croton dichogamus* Pax.

*The scrub land.* The scrub land covers most of the areas around Omisingiyo, Kebololet, Ngama hills, Ol Olojigoshin and hills in the Triangle area. The horizontal density cover ranges between 13·5% to 35·0%. The vegetation is over medium height of 0·6 to 2·0 m (2 to 6 ft). The major grass species are *Themeda triandra*, *Pennisetum meyanum*, *Setaria sphacelata* and *Sporobolus pyramidalis* Beauv. The major woody plants are *Dichrostachys cinerea*, *Acacia hockii*, *Commiphora* sp., *Grewia* sp., *Croton dichogamus*, *Cordia ovalis* DC., *Acacia brevispica* Harms, *Lippia javanica* (Burm. f.) Spreng, *Solanum incanum* and *Maerua edulis* De Wolf.

*Riverine habitat.* This habitat is found along the rivers and streams. It forms a thick cover with a cover height of over 2·0 m. It is found adjacent to the open grassland.

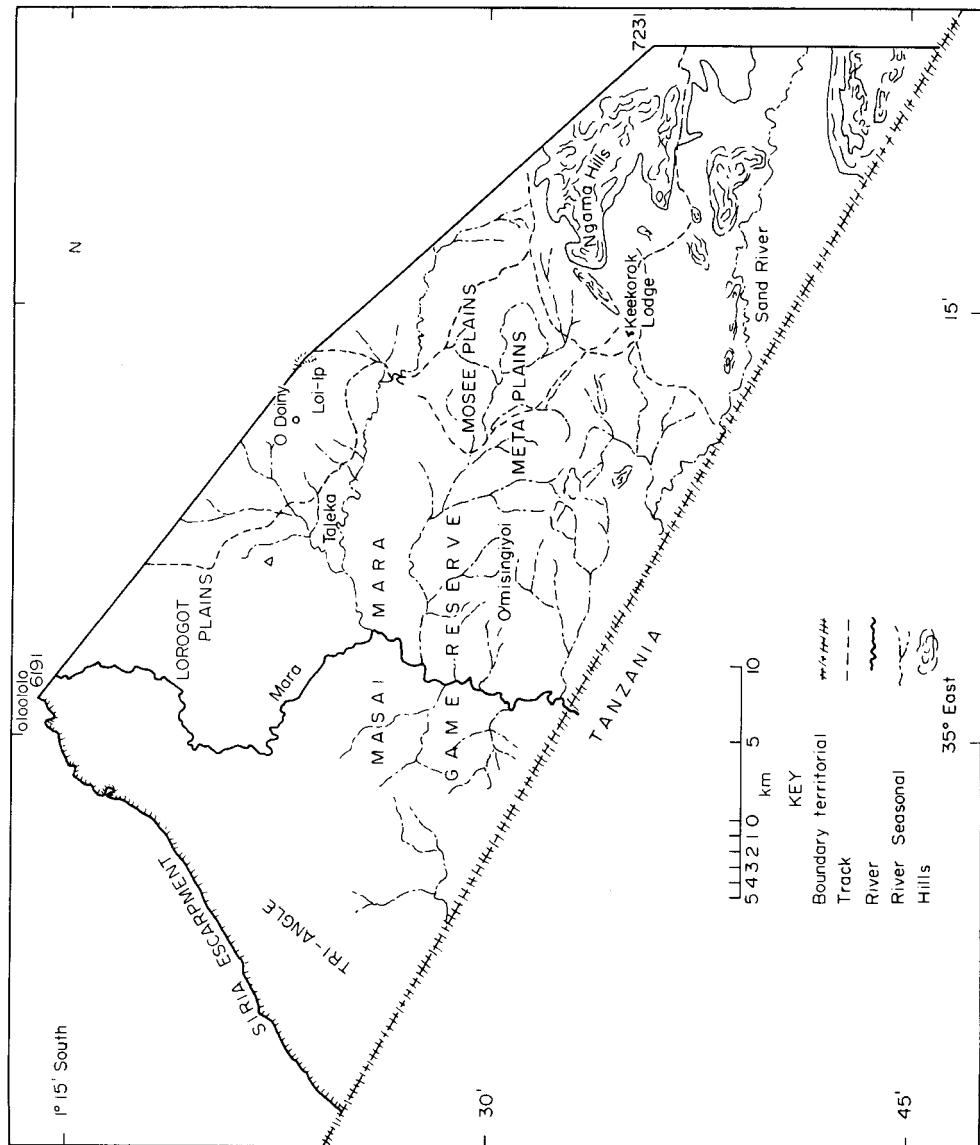


Fig. 2. Study area: Masai Mara Game Reserve.

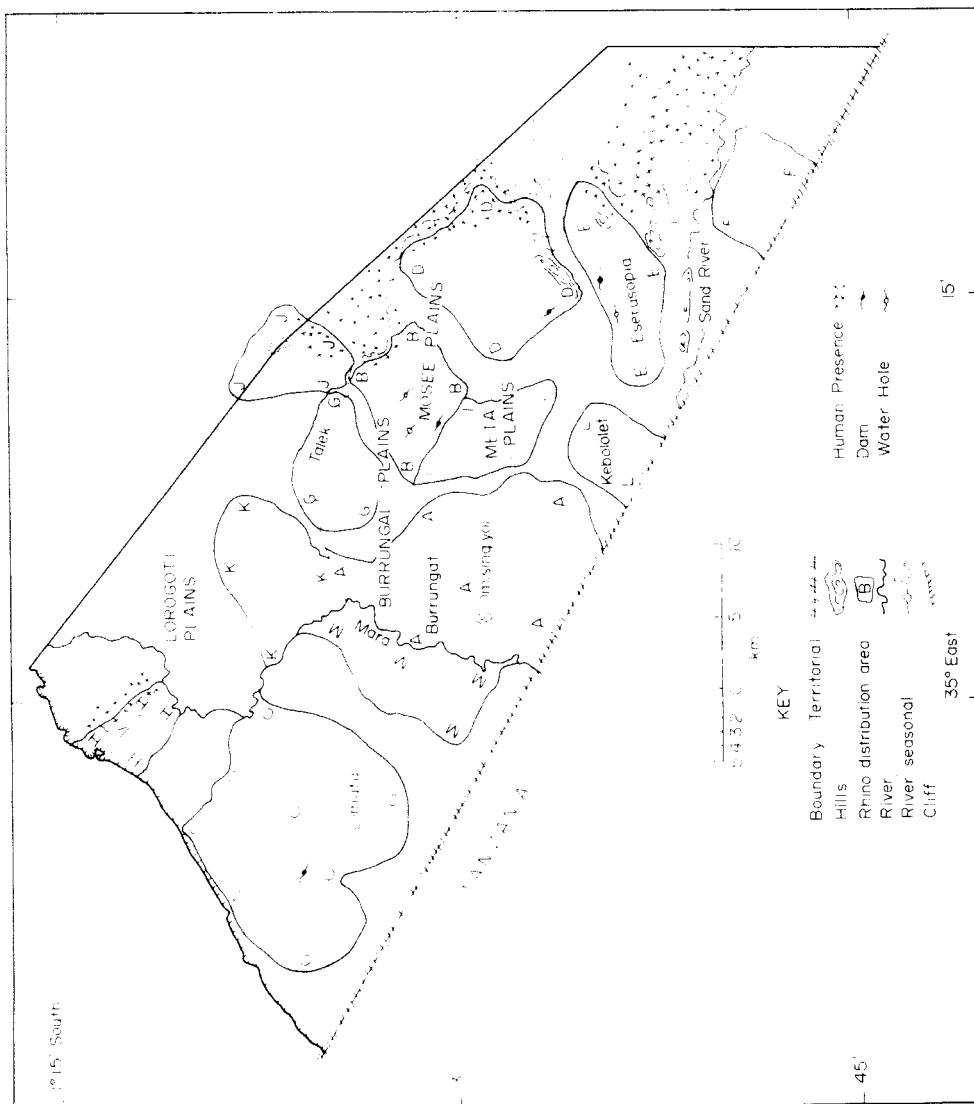


Fig. 3. Rhino distribution areas: Masai Mara Game Reserve.

The main plant species are *Teclea nobilis* Del., *Grewia* spp., *Dombeya* spp., *Olea africana* Mill., *Croton dichogamus*, *Commelina* spp., *Phyllanthus* spp. and *Indigofera* spp.

## Results

### (a) Rhino density

At the end of the study period in August 1972 a total of 108 rhinos had been identified and found to be residents of the Masai Mara Game Reserve occupying thirteen separate areas as shown in Fig. 3.

The rhino density for the entire Reserve is  $0.07/\text{km}^2$  ( $1530 \text{ km}^2$ ), but only  $749 \text{ km}^2$  (area of all distribution areas) of the total area is occupied by rhinos, thus the density within the occupied area is  $0.14/\text{km}^2$ . Density for each 'distribution area' is shown in Table 1. There is very close similarity in densities in distribution areas A and I. In both areas, water is available within a short distance, food is abundant and a large number of thickets for shelter are distributed over a wide range.

**Table 1.** Density, area and number of rhinos in each distribution area

Distribution area	No. of rhinos	Area in $\text{km}^2$	Density per $\text{km}^2$
A	31	133	0.23
B	10	52	0.19
C	14	160	0.09
D	8	52	0.15
E	6	62	0.09
F	3	23	0.13
G	5	30	0.16
H	3	22	0.13
I	11	45	0.24
J	8	52	0.15
K	4	68	0.06
L	1	21	0.04
M	4	23	0.17
Total 13	108	749	0.14 (0.36/sq. mile)

Over 50% of the total rhino population is distributed over the plains. This includes distribution areas A, B, G, I and J whose total number of rhinos is sixty-five, covering an area of  $312 \text{ km}^2$ . The density of rhinos on the plains is  $0.21/\text{km}^2$ .

The other distribution areas together have forty-three rhinos covering an area of  $437 \text{ km}^2$ , hence their density is  $0.10/\text{km}^2$ .

The possibility of movement of rhinos out of and into distribution areas was checked and there was no record of a rhino moving from one distribution area to another. Observations indicated that the entire number of rhinos in each distribution area form a resident group for that particular distribution area. Thus the density for each distribution area is consistent all the year round and it can only change due to births of new individuals or deaths of living individual animals.

An aerial count covering distribution areas A, B, D, E, G, I and J was carried out in June 1972 and the result gave a mean density of  $0.18/\text{km}^2$  on the basis of area flown.

(b) *Distribution*

As indicated by the number of rhinos found in each distribution area (Table 1) rhinos were not equally distributed. The distribution areas were not separated by any major barriers except for the Triangle area where the Mara river separated distribution areas in the east from those in the west. The influence of habitat on distribution, particularly availability of food, water, and cover, and human interactions was investigated.

*Food availability.* Plants commonly eaten by rhinos were found to be present in each distribution area though not in equal amounts. However, during the burning period, there is a shortage of food. As soon as rain falls regeneration of vegetation is observed over all burnt areas. Throughout the study period rhinos were observed feeding mainly on branches of regenerating herbs and woody plants.

Despite fluctuations of food availability during burning periods, statistical analyses indicate that in the most important distribution areas, density of rhino is significantly ( $P < 0.05$ ) related to the density of known food plants. This is shown in Fig. 4, where

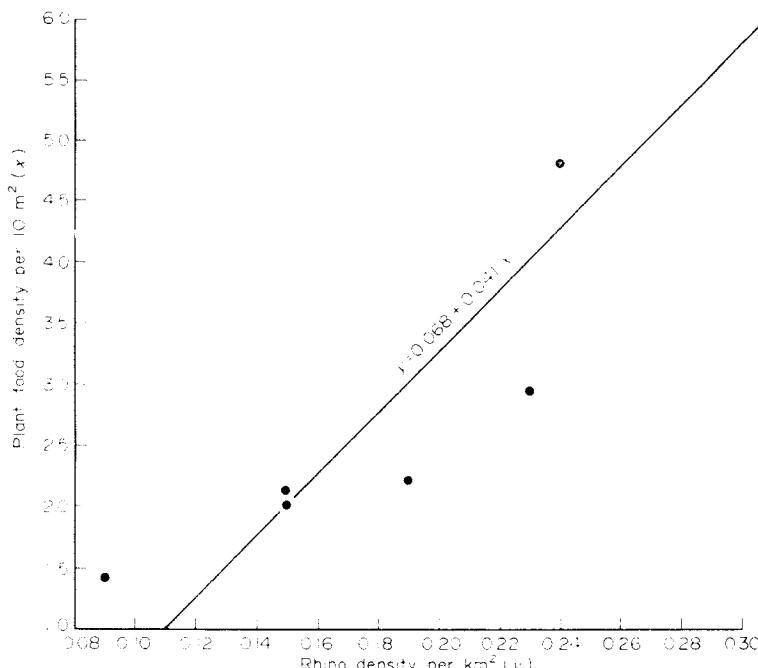


Fig. 4. Regression of plant food density per 10 m<sup>2</sup> on rhino density per km<sup>2</sup>. ●, Most important distribution areas.

the densities of rhinos in the six most important distribution areas, between them containing 76% of the Mara rhino population, are plotted against density of known food plants in each distribution area. For these areas the slope of the regression is significant ( $P < 0.05$ ) and is expressed by:

$$y = 0.068 + 0.041x$$

where  $y$  is rhino density in individuals/km<sup>2</sup> and  $x$  is known food plant density in individuals/10 m<sup>2</sup>.

$$s = 0.0307$$

$$t = 3.582$$

*Water.* Permanent water supplies are abundant during the rainy period in each distribution area, however during the dry period the main sources of water are dams, water holes, standing water along dry streams and rivers and main rivers. Some of these water sources are widened wallowing holes along the Sand and Talek rivers, and streams along Siria Escarpment. In some distribution areas sources of water are within a short distance of rhinos while others have widely spaced water sources.

*Cover.* Cover may be the major cause of the present pattern of rhino distribution in Mara. Statistical analyses indicate that density of rhino is significantly ( $P < 0.01$ ) related to the proportion of 'open' grassland in each distribution area and therefore density of rhino is significantly negatively related to the proportion of thickets and wooded grassland. The relationship between rhino densities in distribution areas and the proportion of grassland in each is shown in Fig. 5. Two regression lines have been drawn, one for all distribution areas, and the other for only the six most important

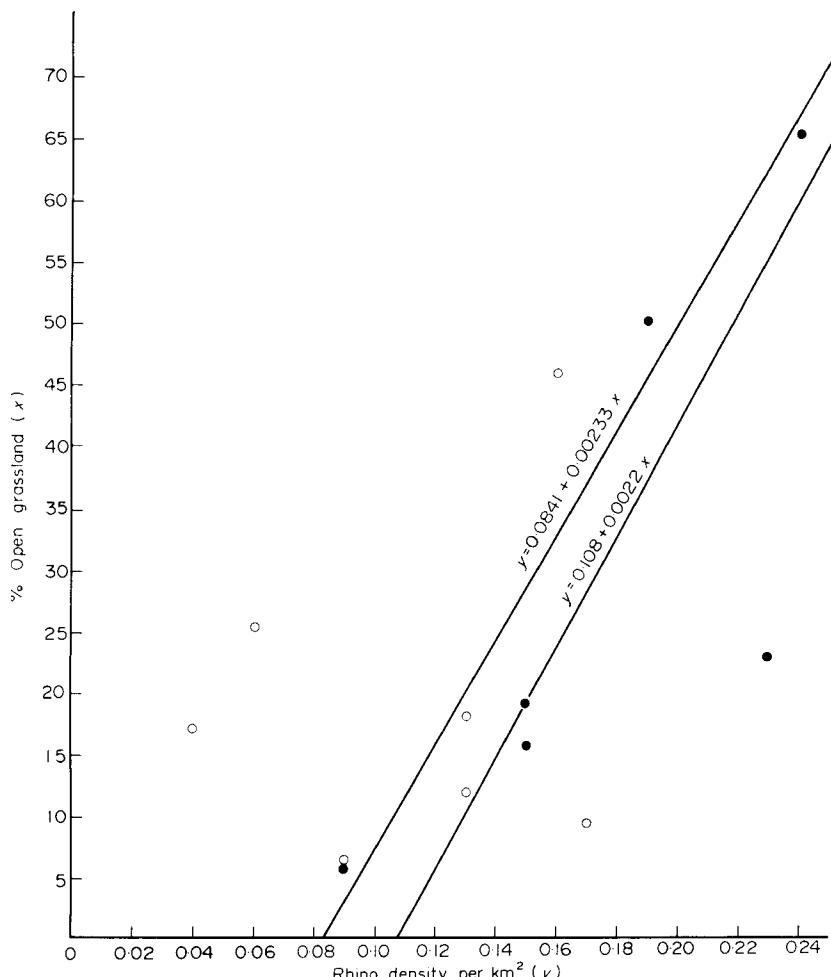
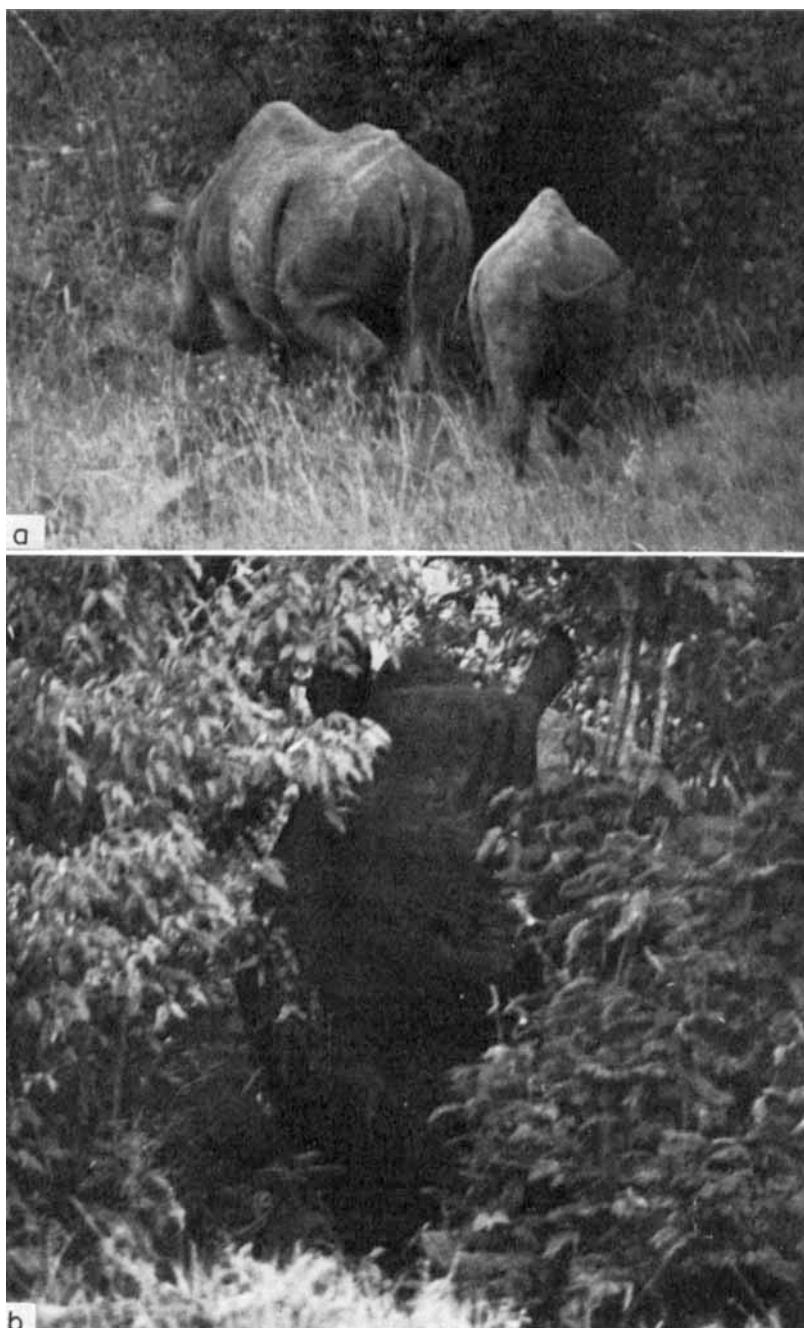


Fig. 5. Regression of percentage open grassland on rhino density per  $\text{km}^2$ . ●, Six important distribution areas; ○, seven less important areas.



**Fig. 6.** (a) Female rhino accompanied by a calf running into the bush for cover after an alarm. (b) A male rhino which had run into the bush trying to find the direction of the alarm.

(distribution areas A, B, C, D, I and J). The slopes of each are significant ( $P < 0.01$  and  $P < 0.02$  respectively) and their formulae are:

All distribution areas:

$$y = 0.084 + 0.0023x$$

$$s = 0.045; t = 3.23; \text{d.f.} = 11.$$

Six most important distribution areas:

$$y = 0.108 + 0.0022x$$

$$s = 0.0265; t = 4.33; \text{d.f.} = 4.$$

Where  $y$  = density of rhino in individuals/km<sup>2</sup> and  $x$  = proportion of grassland in the distribution areas as percentage.

Most of the feeding observations were made on open grassland and wooded grassland where rhinos' preferred food plants occur.

In over 90% of the observations when rhino were disturbed by man on foot, in a car or an aircraft, they ran into dense bush where they stood watching and flapping their ears as shown in Fig. 6. It was observed that it was difficult to drive them out of the bush.

The rhino is a sedentary animal which needs thick cover in which it can rest after feeding and wallowing.

*Human interactions.* Human presence was also noted to affect the distribution of rhinos. No rhino was observed living close to the areas used for grazing and occupied by Masai tribesmen. These areas, as shown in Fig. 3, include areas close to distribution areas B, D, E, F, H and J.

### (c) Population structure

*Size and composition.* Of the 108 rhinos in the Mara population, 73% were adults and 23% were immatures. At least an adult and an immature were found in nearly all distribution areas. Size and composition for each distribution area is shown in Table 2.

*Sex ratio.* Among the 108 rhinos in the study area ninety-seven (87.3%) were sexed. The results show that the entire Mara population comprise 38.7% adult males and 32.4% adult females. Of all immature animals eleven (40.0%) were not sexed. The

**Table 2.** Percentage of total population of rhinos found in each distribution area

Distribution area	Total population (%)	Adult male (%)	Adult female (%)	Immature both sexes (%)
A	28.8	9.9	10.8	7.2
B	9.0	3.6	3.6	1.8
C	12.6	5.4	3.6	3.6
D	7.2	3.6	2.7	0.9
E	5.4	1.8	2.7	0.9
F	2.7	0.9	0.9	0.9
G	4.5	0.9	1.8	1.8
H	2.7	0.9	0.9	0.9
I	9.9	4.5	2.7	2.7
J	7.2	1.8	2.7	2.7
K	3.6	1.8	0.9	0.9
L	0.9	0.9	—	—
M	3.6	1.8	0.9	0.9

ratio of males : females is 1·2 : 1 (fifty-five males and forty-two females). However, the ratio of the adult males : adult females (forty-two adult males and thirty-eight adult females) is approximately 1·1 : 1, but for the immature rhinos the result may not be representative and cannot be interpreted with confidence.

*Age structure.* The results show that the Mara rhino population has 7·2% of rhinos in Age Class I, 7·2% in Age Class II, 11·7% in Age Class III and 73·0% in Age Class IV. Age Class IV comprises 54% males and 46% females. Out of the entire adult females, 75% were accompanied by the calves (twenty-eight calves) which formed Age Class I, II, and a few in Class III.

Age structure for each distribution area is shown in Table 3. It needs to be remembered that if individual rhinos in age class IV had their actual age known they would have been grouped into various age classes since they were not all of the same age.

**Table 3.** Age structure in each distribution area

Distribution area	No. of rhinos and age classes				% of total population and age classes			
	I	II	III	IV	I	II	III	IV
A	2	2	4	23	1·8	1·8	3·6	20·7
B	—	2	1	7	—	1·8	0·9	6·3
C	3	—	1	10	2·7	—	0·9	9·0
D	—	—	1	7			0·9	6·3
E			1	5			0·9	6·3
F			1	2			0·9	1·8
G		1	1	3		0·9	0·9	2·7
H		1		2		0·9		1·8
I	2	1		8	1·8	0·9		7·2
J	1	1		5	0·9	0·9	0·9	4·5
K			1	3			0·9	2·7
L				1				0·9
M			1	3			0·9	2·7
Total 13	8	8	13	79	7·2	7·2	11·7	73·1

*Mortality.* Only one adult rhino died during the study period. No record was made of mortality of juveniles and sub-adults. However, the Warden in charge of the Reserve reported that eleven rhinos have been found dead since 1963.

#### (d) Social organization

Various aspects of social organization were studied, such as group composition and seasonal changes. Further work was done on group size, influence on numbers in a group and territoriality.

However, I find information on sizes of home ranges relevant to density and distribution of the Mara rhinos.

*Home range size.* Home range sizes were determined for five males, two lone females and five females with calves (Table 4). These sample sizes are too small for statistical demonstration of absolute differences between average home range sizes for these social classes. However, Joubert & Eloff (1971) and Goddard (1967) have both stated that the home ranges of immatures and females with calves are larger than single males and females. My data suggest that this may be true of the Mara population.

Table 4. Range size and overlap of study animals

Rhino No.	Sex	Distribution area	Range size (km <sup>2</sup> )	Overlap area (km <sup>2</sup> )
3	Male	A	7.12	0.88
4	Male	A	6.64	4.92
7	Male	B	13.32	12.48
14	Male	E	14.92	7.92
27	Male	B	18.60	2.64
10	Female	B	12.72	11.68
15	Female	E	14.92	7.92
1A	Female (+)	A	13.60	5.80
8A	Female (+)	B	22.68	12.48
17A	Female (+)	E	17.32	7.92
43A	Female (+)	J	5.60	0.08
56A	Female (+)	J	9.52	0.08

(+) = Female accompanied by a calf.

If comparisons are made within the same distribution areas, thus nullifying effects of differences in habitat factors, females with calves do appear to have used larger ranges: for example rhino 1A with rhinos 3 and 4 in Distribution Area A, and rhino 17A with rhinos 15 and 14 in Distribution Area E. I also suggest that some single males and single females use almost the same ranges and the possible 'within Distribution Area' comparison in Table 4 (rhino 7 with 10 and 14 with 15) supports this. However, on the whole, disregarding whether a female has a calf or not, females' home ranges are larger than males as shown by a 'within Distribution Area' comparison in Table 4 (rhino 1A with rhinos 3 and 4 in Distribution Area A; rhinos 8A with 7 and 27 in Distribution Area B, and rhino 17A with 14). Male rhino number 14 was always physically in the company of female number 15 and also male number 7 was mostly located together with female number 10 and the comparison for their home range sizes were therefore similar.

#### *Influence on the size of home range*

*Difference within group units.* In general, single males and single females had smaller size of home range than females with young. This is probably because single males and females are solitary and spend most of their day time resting in the bush, hence their movements are within the areas around the sheltering places. However, females with young tend to move more looking for food and probably acquainting calves with other areas within the home range.

*Overall influence of habitat type on home range size.* There was not much difference in the size of home ranges for social group units which used similar habitat. However, it appears that the size of the home range varies considerably according to availability of food, surface water and vegetation for shelter. This was noted on rhinos 1A, 3, 4; 14, 15, 17A; 7, 27, 10, 8A; and 43, 56A.

*Other influences on home range size.* Rhinos were observed to move beyond their normal range during the dry periods, mating periods (September–April) and during the burning and after burning when cattle grazing was observed in some areas occupied by rhinos. Rhino movements under the previously mentioned conditions also resulted in home range overlapping.

The degree of home range overlapping is noticeably high particularly within rhinos

in distribution area B. The mean overlapping range for area A was 32.1%, area B 57.1% and area J 1.1%. Considering the entire home range study the mean range overlapping for males is the same as for females with young 49.6% and 46.3% respectively while for single females it is higher with 72.8% overlap.

*Significance of home range.* Rhinos attach themselves to particular areas, here termed home range. A group of overlapping home ranges form distinct separate distribution areas which are not separated by any major barriers (e.g. rivers, escarpments). Figure 7 shows home ranges for individual rhinos which had adjacent home ranges. Also this attachment causes clumps of high densities of rhinos. Almost all rhinos in each distribution area associate with each other but not individual rhinos from another distribution area. This may indicate that rhinos grow up and breed in the parental distribution area so that circulation of closely related genes is likely to occur.

#### Recommendations for rhino management in Mara

##### Burning

Burning is a control method which destroys what is wanted as well as what is not. Mara area is burnt twice a year and when fire starts it becomes uncontrollable and normally burns a considerable area of the reserve at one time.

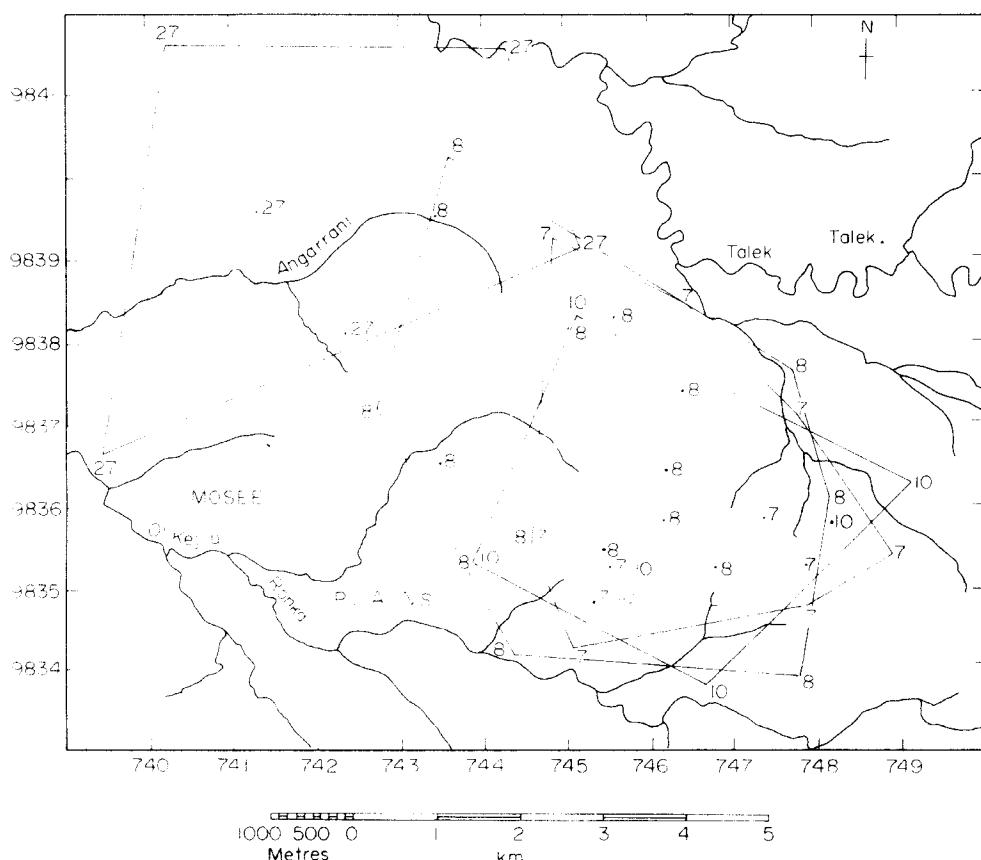


Fig. 7. Rhino home ranges. 8, Rhino points of observation within the home range. >8, Peripheral points of observation.

I suggest that fire barriers be established by improving the existing tracks or constructing other tracks where needed. This may minimize a wide spread of fire. Burning can be done once a year and areas to be burnt need to be selected according to the nature of vegetation. Repeated unplanned burning for some years may destroy the suitable habitat used by the rhinos at present, hence rhinos may be forced to move out of the areas they are occupying now.

#### *Water shortage*

As noted, during the dry periods all the streams and some rivers dry up and rhinos together with other animals depend on water from Mara river, Sand river, Talek river and scattered dams and water holes. The existing water supplies are badly distributed. I feel that earth dams or 'hafirs' should be constructed in Triangle area, Loldurugi, Meta plains, Burrungali plains, Eserusopia and Omissingyoi areas since they are cheap. Preferably three dams in Triangle area and two in other areas.

#### *Human settlement*

Grazing within the Masai Mara Game Reserve is prohibited but nevertheless Masai people are observed grazing their cattle in parts of the reserve close to their Manyattas. Their presence in the reserve affects the distribution and movement of animals. Thus I suggest that these groups of Masai be settled outside the reserve.

#### *Suggestions for further research*

On existing rhino population more prolonged research work is needed on population structure, particularly on aspects of mortality, reproduction and predation, and further investigations on the territoriality concept as it relates to rhino.

#### **Discussion**

The black rhino population in the Mara shows a preference for the open and wooded grassland. Factors contributing to this preference may be availability of food, cover, water and human presence. The data obtained in this study indicate that the density of black rhino in the Mara is especially related to the availability of food, cover and water.

Immature rhinos formed about 25% of the entire Mara population, and over 70% of the adult females were accompanied by calves of different ages ranging up to 4 years. This suggests a stable, high recruitment rate for the Mara population at the present time.

The black rhino is a very sedentary species, and it appears that the size of the home range varies considerably according to the availability of the animal's needs. In distribution area A, where there is a supply of water and green food and cover within easy reach throughout the year, the home ranges are smaller than the home ranges in distribution areas B and E where water supplies are widely scattered.

In general, females with calves cover a larger home range than single adult males or females. However, females appear to have a larger home range than males although in some cases adult males and single females appear to have similar home range sizes.

Black rhino tend to remain attached to some particular areas. The sedentary characteristic has advantages and disadvantages for the conservation of the species. For example, one advantage may be that black rhino can be expected to survive in very small isolated populations in suitable habitats, although surrounded by settled areas.

In Mara, on the other hand, preservation of the present suitable rhino habitat which may gradually be changed by the effect of burning the area twice a year may reduce the danger of eliminating the species in the years to come.

#### Acknowledgment

I want to thank Mr Simon Ole Tipis, Senior Game Warden in charge of Masai Mara Game Reserve for permission granted to do my project within his areas of jurisdiction; Drs C. J. Pennycuick and J. B. Sale for encouraging supervision, comments on methods and corrections on drafts; Mr Simon Taiti for his field assistance; and finally Dr P. J. Jarman for assistance in the analysis and interpretation of the data.

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