HOME RANGE, BEHAVIOUR, AND RECRUITMENT RATES OF TWO BLACK RHINOCEROS POPULATIONS

John Goddard, Biologist, Ngorongoro Conservation Area

Summary

During the period 1964 — 1966 biological studies were conducted of two black rhinoceros *Diceros bicornis* L. populations in northern Tanzania. One population occupies the caldera of Ngorongoro and the other the area in the vicinity of Olduvai Gorge. Detailed records were made of each rhinoceros observation and 182 individuals were seen in the two study areas during the three-year period.

The black rhinoceros is a very sedentary species, and the size of the home range is governed by several factors which are described in the text. The home range of an immature rhinoceros is larger than that of an adult individual. The adult rhinoceros, especially the male, is essentially a solitary animal, but immatures frequently join up with a companion.

Activity patterns are described and illustrated, and are similar in the two study areas. Behaviour of the species follows well-defined patterns, and territorial behaviour is uncommon. Vocal communication in the species is described. The significance of dung piles, used regularly by the species, is considered and the results of experiments using faecal samples are described. Relations with two carnivores are discussed.

The recruitment rates of the two populations are almost identical, i.e. 7.0% at Ngorongoro and 7.2% at Olduvai. Various reproductive characteristics affecting recruitment rates, such as age at maturity, gestation period and interval between successive calves are described using records obtained from zoological gardens and from field observations.

The results of the studies indicate that the rhinoceros population of the Ngorongoro Conservation Area is considerably higher than was formerly believed. The future of the species in the area appears favourable, providing its habitats are not destroyed through encroaching cultivation.

Introduction

During the period 1964 - 1966 an ecological and ethological study was conducted of two discrete black rhinoceros populations in Tanzania. One population occupies the caldera of Ngorongoro and the other occupies the area in the vicinity of Olduvai Gorge. Individual recognition of rhinoceros was achieved by a method involving the use of a photographic record system (Goddard, 1966).

During the study a total of 108 different individuals were seen on the floor of the Ngorongoro caldera, which covers an area of 102 sq. miles. However, on only 14 occasions were animals seen on or adjacent to the rim of the caldera, and these were all individuals which had not been recorded on the floor or walls. This evidence suggests, therefore, that the population on the floor and walls is resident within the caldera throughout the year. The study area at Olduvai is 170 sq. miles and supports a population of 70 animals. The estimated density of the population at Ngorongoro is one rhinoceros per 1.2 sq. miles, and at Olduvai one per 2.5 sq. miles.

The two study areas vary considerably. The caldera of Ngorongoro consists mainly of open grassland interspersed with numerous marshes. Lerai Forest, a small patch of *Acacia xanthophloea* Benth. woodland, supports a very high rhinoceros population. Water is widely distributed and relatively

abundant. The walls of the caldera consist mainly of scrub, with some highland forest on the eastern and south-eastern parts. Typical shrubs growing on the walls are *Lippia javanica* (Burm.f.) Spreng., sodom-apple *Solanum incanum* L. and *Aspilia pluriseta* Schweinf. Annual mean rainfall on the floor of the caldera is 26 in.

The study area at Olduvai on the eastern part of the Serengeti plains is more typical of the thornbush habitat of the black rhinoceros in Masailand. The area is bisected by the gorge which is covered in *Acacia - Commiphora* scrub, with extensive growths of wild sisal *Sanseveria ehrenbergii* Schweinf. The rest of the study area consists of open plains covered with short grassland. Typical trees of the area are *Acacia tortilis* Forsk. and *Commiphora merkeri* Engl. The mean annual rainfall at Olduvai is 16 in., and water supplies are sparse.

Over the three-year period a detailed record was made of each rhinoceros observation and the following data collected. The rhinoceros was identified and the date, time, location, activity of the animal, group association, habitat description and meteorological notes recorded. Other notes, such as the condition of the animal, pattern of water distribution and the presence or absence of avian associates such as the red-billed ox-pecker *Buphagus erythorhynchus* Stanley, were also collected. If the rhinoceros was feeding, it was watched for one hour, and the plants which it selected or rejected were collected and identified. The results of the food-habit studies will be the subject of a separate paper.

The terms "adult" rhinoceros and "immature" rhinoceros are used frequently throughout this paper. An adult animal is used to indicate a full-sized animal. An immature animal is one that is less than full-sized which has left its mother. A calf is considered to be an immature animal which is still with its mother. "Known age" rhinoceros are being marked in the caldera and seven of these individuals have been marked to date. Eight "known-age" calves have been photographed every month over a two year period to provide data on growth rates.

HOME RANGE

Method

The position of each rhinoceros observed was either pin-pointed on an aerial photograph, or its position established by sighting azimuth bearings from three known points on the ground. The size of the home range was calculated by computing the area of a polygon which resulted from connecting the peripheral points of observation of the individual. Size of home range is governed by several factors, which are as follows:

Sex and age class

The mean area of home ranges (in sq. miles) of the two populations is as follows. The figures are calculated from data collected on 66 individuals. (Figures in parentheses following the sex indicate the number in the sample.)

Ngorongoro

Adult ♂	(16)	6.1	(range 1-17.0)
Adult ♀	(13)	5.8	(range 1-10.1)
Imm. ♂	(2)	13.9	(range 5.4-22.4)
Imm. ♀	(7)	10.7	(range 5.5-22.4)

Olduvai

Adult ♂	(11)	8.5	(range 2.1-20)
Adult ♀	(13)	13.7	(range 1.4-35.0)
Imm. ♂	(2)	14.5	(range 11.0-18.1)
Imm. ♀	(2)	8.4	(range 2.9-14.0)

Habitat

This factor is based on a sample of six adult animals (three males and three females) from each of three habitat types: 1) Lerai Forest-green food abundant and water present throughout the year; 2) Central Ngorongoro - open grassland with seasonal marshes; 3) Olduvai - dry *Acacia - Commiphora* bush; water supplies very sparse and widely scattered.

Location	Mean home range (sq. miles)
Lerai Forest	> 1.0
Central Ngorongoro	6.0
Olduvai	11.7

Time of year

This factor is based on a sample of four animals (two males and two females) from each of three habitat types at Ngorongoro according to the season of the year:

Location	Nov.-Apr. (wet)	May-Oct. (dry)
Lerai Forest	> 1.0	> 1.0
Central Ngorongoro	10.7	5.0
Floor-wall (grassland and scrub)	6.9	4.2

Night observations of home range

Only 20 observations of rhinoceros were made at night (Table 1), involving eight animals which all stayed within their established home ranges during the hours of darkness.

Long term observations of home range

It is probable that adult rhinoceros remain attached to their small home range for their entire life, unless translocated by man. Not only were individuals always seen in their particular small area during the study but evidence collected from past years supports this hypothesis. Photographs of 14 different rhinoceros taken at Ngorongoro from two to ten years prior to the study were obtained; ten of these could be identified as animals still present. In seven cases the location in the caldera could also be identified, and in every case the rhinoceros was within the home range it occupied during the study.

Overlap of home ranges

Home ranges of individuals can overlap to a considerable extent, even among adult males. One in Ngorongoro shares 40% of his home range with another adult male. In five adjacent ranges on the caldera floor a mean of 35% of each range overlapped with one or more other ranges.

Seasonal movements within home range

The proportion of the home range which is utilized is considerably greater during the wet season (see above) because of the larger variety of palatable plants available at this time of the year. Clover *Trifolium masaiense* Gillett is extremely palatable to the black rhinoceros, but only at the stage when it is green and succulent; most of the home ranges in which this and other legumes occur are covered extensively by the rhinoceros during the period February-April. In the dry season when the plains herbs are dry and sterile the rhinoceros tends to occupy only the part of its home range in close vicinity to marshes and water. This explains why it is not uncommon for a visitor to see 30-35 rhinoceros at Ngorongoro in one day during the wet season, but only 5-6 during the dry season.

Some rhinoceros tend to be very regular in their movement patterns within their home range. Of the animals for which more than 40 observations are available, approximately 20% could be regularly observed in the same place at the same time. The remainder tended to be more irregular.

Discussion

The data given in the preceding sections indicate that the black rhinoceros is a very sedentary species, but it appears that the size of the home range varies considerably according to the availability of food and surface water. In Lerai Forest where there is a supply of green food and water throughout the year, the species is extremely sedentary and densities can be as high as 23/sq. mile. Only six of the 23 animals which have been seen using the forest have ever been seen outside and the remaining 17 could always be located inside. At Olduvai where water supplies are widely scattered the mean home range is considerably larger. However, there is some evidence from Olduvai that some rhinoceros can survive without free water.

In general immature animals cover a larger home range than adults (see 'sex and age class'). When the rhinoceros gives birth to a new calf she will not tolerate the presence of the previous calf (see section on group structure p. 138). The discarded calf tries to join up

with another rhinoceros as soon as possible, and if tolerated it normally stays with its new companion. The immature animal may join with an adult whose home range overlaps its own, but which extends further afield. The movements of the immature animal are governed by the adult, thereby extending the former's range into new areas. The observations also indicate that immature rhinoceros, even when solitary, tend to wander further than adults. These factors (the larger home range of the immature animal, and the intolerance of the mother for her old offspring) may serve an evolutionary function, assuring population dispersal in a species which is very sedentary and therefore susceptible to the effect of inbreeding.

Because of the fact that the rhinoceros tends to remain attached to some particular area, the claims of some of the older residents of East Africa that the species has been completely shot out in some regions are probably true. Population dispersal from adjacent inaccessible areas into the available niches created by mortality from hunting is probably extremely slow; it can be seriously questioned if it occurs at all among the surviving adult population.

The sedentary characteristic has advantages and disadvantages for the conservation of the species, which may be expected to survive in small isolated populations in suitable habitats, even though surrounded on all sides by cultivated areas.

Boundaries of national parks and game reserves are usually established by some convenient reference to topography, roads or watercourses, and rarely consider migratory patterns of the animals which utilize the park. The black rhinoceros is a species which may be least affected by this and it would be expected to receive adequate protection in well-patrolled game parks. However, the regular habits of some individuals make them extremely vulnerable to poaching by men who are familar with their habits and daily movement patterns.

ACTIVITY PATTERNS

When a rhinoceros was observed, its major activity at the time was noted. Four major activities were recorded, i.e. feeding, walking, sleeping (lying down) and standing, and other activities such as wallowing, drinking, fighting, mating and defecating were noted when observed. In this way 2227 different activity observations were made in the two study areas during the three-year period. The total number of observations during each one-hour period of the day was obtained from the field records, and the percentage of these observations occupied by the major activities is shown in Tables 1 and 2. Observations of males and females are considered separately, and the records include adults and immatures.

Figure 1 illustrates the diurnal activity pattern of the two populations; the data from Tables 1 and 2 are used to show, in relation to the time of day, the proportion of observations in which animals were active (feeding or walking) or inactive (sleeping or standing). It can be seen that from 0600-0700 hours over 80% of all the rhinoceros were active, but by 1200 hours this figure had dropped to about 30%. Between 1100-1400 hours there was a slight rise in activity, followed by a fall to the previous level. After 1400 hours the activity rose steadily, approaching 100% by 1900 hours. The limited number of nocturnal observations (20) suggest that the majority of the population is active at night, although some individuals sleep during the hours of darkness.

Wallowing

More than 90% of the observations of wallowing rhinoceros were recorded between 1600 and 1800 hours. The wallowing animal usually smears itself with mud on both sides of its body, and sometimes rolls over on to the spine. This is undoubtedly a method of cooling, and disposes of excess heat accumulated in the body during the day.

Resting

The absence of shade does not appear to affect the black rhinoceros adver-

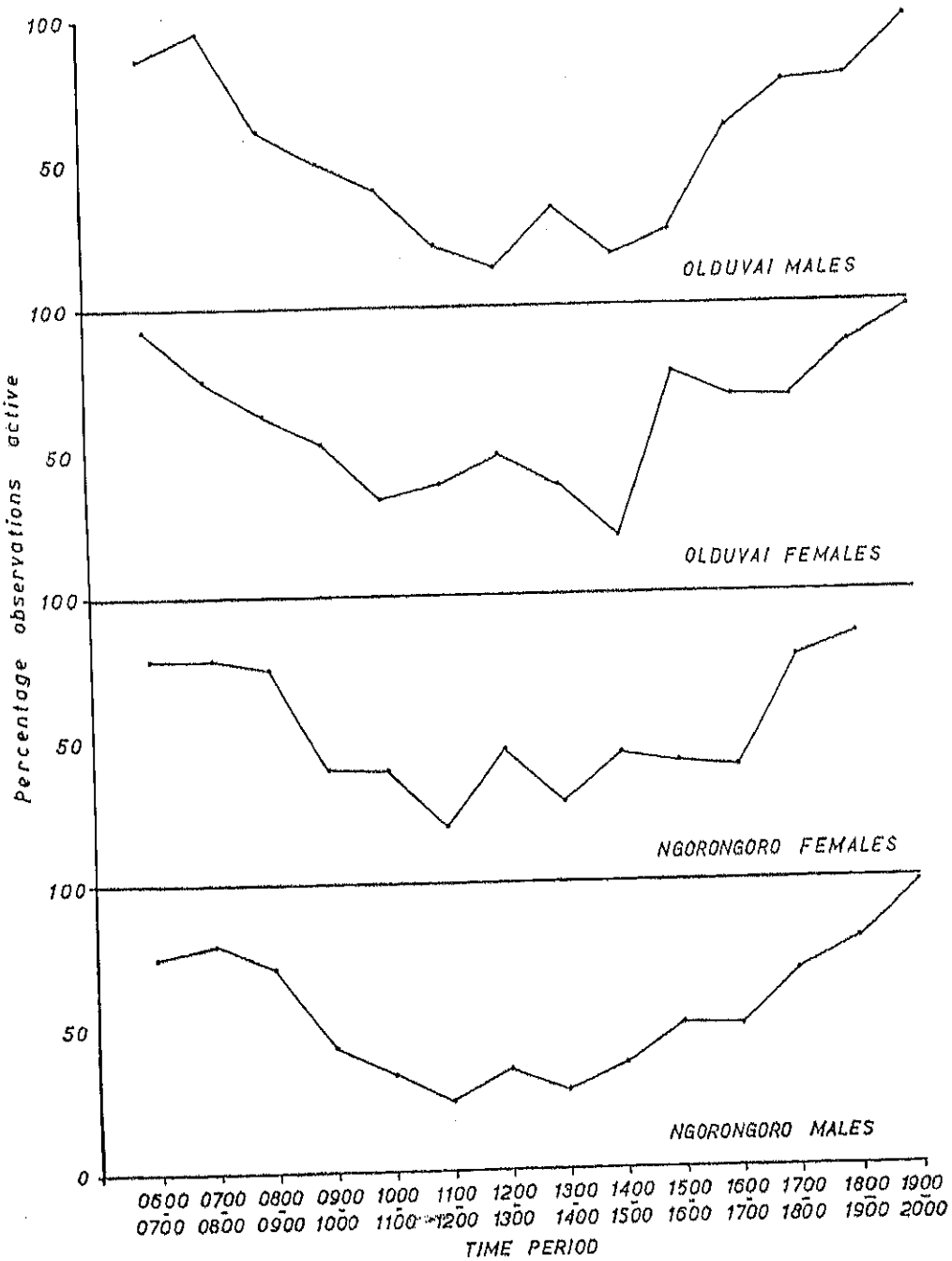

Figure 1

Diurnal activity of two black rhinoceros populations.

sely. At Olduvai individuals have been observed lying in extremely hot sun less than 20 yards from ample shade offered by an umbrella acacia. However, the animal shows a marked preference for sleeping in sand or dust depressions, and will frequently use the same bed for resting.

Resting rhinoceros usually lie upright on their sternum; lying on the side is seen much less frequently (0.5% of the observations) and usually in calves. Resting rhinoceros stand at regular intervals, apparently to relieve the somewhat cramped posture of sternal recumbency. One resting rhinoceros was watched continually for a ten hour period. Approximately every 90 minutes the animal stood for periods of 10-15 minutes, before relaxing again into the typical resting attitude.

Walking and feeding

During the wet season most of the rhinoceros at Ngorongoro make extensive use of the plains part of their home range, feeding on clover or the new flush of green shrubs. Thus they are out in the open and relatively easy to observe. When sleeping or resting, which they often do for most of the day, they remain in the open. In the dry season the "central" population is still located in the centre of the caldera, but they spend a considerable amount of time in the marshes feeding on aquatic plants. Little use is made of the plains part of the home range as palatable fresh shrubs are not available. In the morning they lie down in the marshes, frequently among tall reeds, and thus are difficult to see. Part of the "peripheral" population descends onto the caldera floor at night in order to obtain water. In the wet season the plains part of their home range contains luxuriant growths of clover and shrubs, and they feed on the plains area, sometimes all night. In the early part of the morning they lie down where they have been eating. In the dry season, although some come down to obtain water, there is very little palatable food on the plains. They thus return well before daybreak to the thick growth of shrubs on the caldera slopes to feed, and by the time they lie down they are usually among dense bush and thus concealed from view. However, even at the height of the dry season, they can still be located on the caldera walls. A similar pattern, with regard to the use of the bush and plains part of the habitat, exists at Olduvai.

GROUP STRUCTURE

Composition of group structure of the two rhinoceros populations is shown in Table 3. As shown in the table, the adult male rhinoceros is essentially a solitary animal; however it is seen with other animals of both sexes and all ages. One adult male at Ngorongoro was seen regularly in the company of a 15 month female and another has, at different times, been seen with five different females. The adult female also tends toward a solitary existence with her calf, but not as much as the adult male; the adult female is usually more tolerant to the presence of another immature animal other than her calf.

Immature rhinoceros are seen alone but attach themselves to other individuals, especially other immature animals and adult females, as frequently as possible. This is very apparent at Ngorongoro (see Table 3), and to a lesser extent at Olduvai, but the smaller number of observations in the latter study area prevent an adequate comparison. The largest group of rhinoceros I have seen together consisted of 13 animals, but the group disbanded after two hours into solitary animals and groups of two and three.

As mentioned earlier, the female rhinoceros will not tolerate her old calf when the new offspring arrives. This has been witnessed on 13 occasions in the two study areas. In each instance a female was observed in company with her very large calf. On subsequent dates the calf was observed by itself. An intensive search for the mother produced, on all occasions, a record of her with a tiny new calf. The discarded calf invariably attempts to join up with a new companion as soon as possible.

TABLE 1

Major activity patterns of the black rhinoceros in Ngorongoro caldera

Time period	Males					Females				
	Total observ.	%feeding	%walking	%sleeping	%standing	Total observ.	%feeding	%walking	%sleeping	%standing
0600–0700	58	41	31	7	21	50	34	44	8	14
0700–0800	69	45	34	9	12	66	51	26	9	14
0800–0900	38	26	45	18	11	51	33	41	16	10
0900–1000	55	27	15	40	18	31	29	10	48	13
1000–1100	77	18	17	43	22	55	13	27	33	27
1100–1200	75	16	7	57	20	41	12	7	49	32
1200–1300	52	21	11	39	29	35	26	20	23	31
1300–1400	64	12	16	60	12	51	20	8	51	21
1400–1500	87	23	14	42	21	48	26	17	40	17
1500–1600	87	33	17	31	19	69	35	6	45	14
1600–1700	93	29	20	37	14	85	33	6	40	21
1700–1800	97	46	23	25	6	103	60	17	11	12
1800–1900	38	37	42	18	3	47	45	38	13	4
1900–2000	2	50	50	—	—	—	—	—	—	—
2000–2100	—	—	—	—	—	—	—	—	—	—
2100–2200	1	100	—	—	—	—	—	—	—	—
2200–2300	2	—	50	50	—	2	—	50	50	—
2300–2400	3	—	67	33	—	2	—	—	50	50
2400–0100	1	—	—	100	—	1	—	—	100	—
0100–0200	1	100	—	—	—	1	100	—	—	—
0200–0300	—	—	100	—	—	1	100	—	—	—
0300–0400	1	—	100	—	—	1	—	100	—	—
0400–0500	—	—	—	—	—	—	—	—	—	—
0500–0600	—	—	—	—	—	1	—	—	100	—
Total	901					741				

TABLE 2

Major activity patterns of the black rhinoceros in Olduvai gorge

Time period	Males					Females				
	Total observ.	%feeding	%walking	%sleeping	%standing	Total observ.	%feeding	%walking	%sleeping	%standing
0600–0700	15	60	26	7	7	32	59	32	3	6
0700–0800	19	48	47	—	5	41	37	37	12	14
0800-0900	31	35	26	26	13	39	39	23	18	20
0900–1000	18	28	22	45	5	23	39	13	26	22
1000–1100	12	8	34	50	8	21	5	28	62	5
1100–1200	15	7	13	53	27	16	7	31	31	31
1200–1300	8	—	13	74	13	19	27	21	31	21
1300–1400	3	33	—	67	—	8	25	12	25	38
1400–1500	6	—	17	50	33	11	19	—	36	45
1500–1600	12	25	—	67	8	16	64	12	12	12
1600–1700	19	42	21	21	16	46	50	17	17	16
1700–1800	49	51	27	8	14	47	32	36	15	17
1800–1900	32	41	38	12	9	25	44	44	—	12
1900–2000	—	—	—	—	—	2	—	100	—	—
Total	239					346				

BEHAVIOUR

Greeting behaviour of rhinoceros follows a well-defined pattern and when the apparent intruder has been accepted, or its close presence tolerated, the interest of the individuals in one another gives way to indifference or mutual tolerance.

Greeting between male and female

When an adult male encounters a female, either or both animals may emit the characteristic "puffing snort". The male then approaches the female, taking short cautious steps, occasionally thrashing his head from side to side in a sweeping motion or "rooting" the air with the anterior horn. If the female responds, either by approaching the male or charging him, the latter wheels around and gallops in a small circle, only to return to the female with the cautious short step approach. The male occasionally feeds during the approach to the female. This behaviour continues for several hours, until one of the animals walks away. Aggression of the adult male towards the calf sometimes occurs. The calf usually stays near the female, but if the female is distracted the male may attempt a charge at the calf. On one occasion, the adult male concerned separated the calf from the female, and proceeded to chase it, jabbing its anterior horn viciously between the calf's hind legs. The male finally knocked the calf over, and gored it between the hind legs. Only when the calf started to squeal did the female take offensive action against the male.

Greeting between females

When two females meet there is little aggression, but the approach to one another is extremely cautious. When contact is made they usually nudge one another gently with the sides of the head, or joust with the anterior horns. Tolerance is usually followed by indifference, and one or the other usually walks away.

Territorial behaviour

The black rhinoceros occupies a well defined home range but, as indicated, ranges may overlap to a considerable extent. Individuals of a community, i.e. animals which share common parts of their home range and which in the course of their travels come in frequent contact with one another, are not usually aggressive to one another. In seven instances, two adult males which share part of their home range were observed lying side by side or gently nudging one another with the sides of their heads. Adult females occupying adjoining home ranges show a similar tolerance towards each other.

Hence territorial behaviour among individuals of a community is not apparent in the species. However, if a "stranger" of either sex enters the community territorial tendencies may become apparent, especially if the conflict of interest concerns two adult males. In the caldera of Ngorongoro some rhinoceros occasionally descend on to the floor well outside their normal home range to obtain salt from the alkaline pans, and should contact be made with another male rhinoceros violent aggression may ensue. The resident rhinoceros invariably attacks and is extremely vocal. The head is lowered, eyes rolled, ears flattened, tail raised, and the animal curls its upper lip, emitting a screaming groan. The stranger is invariably silent and on the defensive, but repels the vicious charges of its opponent. The anterior horns are used for goring, or for clubbing the other animal on the sides of the head. If the intruder retreats, he is pursued, sometimes for up to a mile. In all but one case I witnessed, the intruder left the disputed area and returned to his usual haunts. In this single case the intruder drove the resident male out, and the latter is now occupying the adjacent home range. Aggression of this kind was witnessed between an adult male and a strange female, but aggression between the two was not as violent nor as prolonged as that between two males.

Vocal communication

Vocal communication has been observed in the two populations. If a female and calf become separated (e.g.

TABLE 3

Group structure of 146 rhinoceros at Ngorongoro and Olduvai

	No. of individuals	Observations: Total	Observations: Mean per individ.	Group structure *: Solitary	Group structure *: With adult Male	Group structure *: With adult Female	Group structure *: With Immat.
			Ngorongoro				
Adult ♂♂	37	647	17.5	78.7%	4.3%	10.5%	6.5%
Adult ♀♀+	29	476	16.4	74.8	10.9	5.4	8.9
Immat. ♂♂	9	143	16.0	56.0	0.1	7.0	36.9
Immat. ♀♀	12	211	17.6	30.6	13.3	21.9	34.2
			Olduvai				
Adult ♂♂	22	182	8.3	81.5	0.0	15.1	3.4
Adult ♀♀+	19	278	14.6	78.0	9.1	5.6	7.3
Immat. ♂♂	10	55	5.5	59.9	2.3	32.3	5.5
Immat. ♀♀	8	44	5.5	79.0	6.2	13.5	1.3

* Mean per cent. of total observations on each individual.

\+ "Solitary" in the case of adult females includes animals with calves in addition to animals which were entirely alone.

when the calf is sleeping and the mother is browsing some distance away), the female emits a very high-pitched "mew" barely audible to the human ear. The calf reacts immediately and walks toward the direction of the call. An imitation of this sound is sometimes effective in calling a rhinoceros, and is useful in very thick bush when trying to identify an individual.

When a calf is in distress it emits a bellowing squeal. In three instances during the immobilization of a rhinoceros, the calf of the immobilized animal emitted this squeal when separated from the mother and caught with ropes. The squeals stimulated immediate reaction from other rhinoceros within hearing distance; these immediately rushed toward the source of the sound.

Defecation

During the study period all rhinoceros dung piles found were recorded and mapped. Some were pinpointed on the ground by placing a white stone in the vicinity of the pile. If these deposits are territorial markers one would expect that they would tend to be located on the peripheral parts of the territory. In fact, dung piles are located more or less at random over the home range. The same dung pile may be used by several individuals of both sexes, but they do not defecate on every dung pile which they approach.

When individuals approach a dung pile, their behaviour is similar. The deposit is sniffed extensively and the upper lip and base of the anterior horn may be thrashed from side to side in a wide sweeping motion. Occasionally the deposit is "rooted" with the anterior horn. Males have a more marked tendency to "sweep" the deposit. The animal may shuffle through the dung pile keeping the front and hind legs rigid. After defecation, the dung is invariably scattered with sharp kicking motions of the hind legs. The kicking of the deposit sometimes occurs during actual defecation, but more often after the total deposit has been dropped. Small thorn trees in the vicinity of the pile are sometimes demolished after defecation.

The rhinoceros is able to follow faecal scent trails with considerable accuracy and this is probably the method it uses to orient itself within its home range. It is also probably used to keep contact with other rhinoceros. On many occasions rhinoceros have been observed following each other, with at least a mile between them. Both animals appeared to be following an identical course. Since observations of their behaviour, and their poor eyesight, suggest that rhinoceros are particularly dependent on their olfactory senses, their ability to follow scent trails was tested as follows. Samples of faeces a) from the animal being tested, b) from others with home ranges overlapping with that of the experimental animal, and c) from animals with home ranges some distance away were placed in carefully washed new net bags. The bag was then attached to the end of a 75 yd rope and towed behind a Land-Rover as close as possible to the experimental animal. Reactions of animals to artificial deposits of the three kinds of faeces were also tested.

Results of experiments on ten animals using faecal samples are shown in Table 4 : 60% followed scent trails of their own dung and 50% defecated on an artificial deposit of their own faeces; 70% followed scent trails of dung from animals with which they shared a home range, but only 20% defecated on artificial deposits of these animals. Only 30% followed scent trails of dung taken from animals several miles distant and 30% defecated on deposits from these animals.

On one occasion a dung sample was collected from a rhinoceros and introduced to the same animal 48 hours later; the sample was then towed for a distance of just over two miles. The trail was zig-zagged to determine if the animal actually followed the set trail, which it did exactly, and 38 minutes later it was alongside the Land-Rover still sniffing the trail laid by the sample.

Although the results are inconclusive, it may be that the rhinoceros has some method of recognizing dung deposits and scent trails of various animals with which it shares a home range.

TABLE 4

The effect of introducing artificial scent trails and dung deposits, made from samples of faeces, to ten rhinoceros

Rhinoceros	Sample from same animal		Sample from animal sharing home range		Sample from distant animal	
	Scent trail	Dung pile	Scent trail	Dung pile	Scent trail	Dung pile
1	+	+	+	—	—	—
2	+	+	+	*	—	+
3	+	+	—	+	—	—
4	+	+	+	—	+	+
5	—	—	+	+	—	—
6	—	—	—	—	—	—
7	+	—	+	—	+	+
8	—	+	+	*	—	—
9	+	—	—	—	+	—
10	—	—	+	—	—	—

\+ animal followed the scent trail or defecated in the artificial deposit.

* urinated on artificial deposit.

— negative reaction to the scent trail or deposit.

While walking, some individuals urinate frequently. If the place of urination is examined the remains of an old dung pile can sometimes be detected. The significance of kicking the dung is still not clear, but a likely explanation is that kicking, and actual shuffling through dung piles, smears the hind feet with dung which leaves a scent trail imprinted behind the walking animal. When the feet of immobilized animals were examined the characteristic odour of the dung pile could always be detected.

A record of the ability of young rhinoceros to orient themselves was obtained at Ngorongoro during the immobilization of an adult female. The animal was darted and an attempt made to immobilize and tag her 14 month calf. When the mother collapsed the calf, in company with another immature animal, made off rapidly and disappeared into Lerai Forest, some six miles beyond the periphery of the home range of its mother. Both animals were still in the forest at nightfall, but at 0615 hours the following morning they were observed in their usual home range.

PREDATION

On seven occasions I have seen black rhinoceros approach lion *Panthera leo* Neumann. On all occasions the former walked toward the pride as soon as it became aware of the pride's presence. The lions continued to lie down until the rhinoceros was about ten yards away, but then moved away.

The rhinoceros is vulnerable to predation by lion, even when adult (Ritchie, 1963). Proven cases are, however, rare. One attempt by a lion to kill an 11-month old rhinoceros was observed in Ngorongoro on 7th August, 1966. At 1030 hours three sub-adult male lions

were seen watching a rhinoceros with her calf. One lion got up and approached them. As he neared the animals he broke into a run. The calf snuggled against its mother, who moved toward the approaching lion. The calf retreated and the lion pursued it, separating it from the female. The mother followed the pursuing lion at a steady trot, and the calf doubled back to the female. The adult immediately engaged the lion, who diverted his attention to her. He bit her just above the hock, attempted to hang on, and clawed her thigh. The female wheeled around with incredible speed and gored him twice in the centre of the ribs, using the anterior horn with quick stabbing thrusts. The lion rolled over, completed winded. The rhinoceros then gored the lion once in the centre of the neck, followed by another thrust through the base of the mandible, killing him instantly. The two other lions had not moved during the entire proceedings.

Rhinoceros appear to be vulnerable to predation by the spotted hyaena *Crocuta crocuta* Erxleben up to the age of about four months. Three attempts by hyaenas to pull down such animals were observed, all unsuccessful. On one occasion a hyaena grabbed the calf's tail and another the hind leg. The calf tried to shake them off, but when this proved unsuccessful it emitted the distress squeal. The female, who had been walking ahead, reacted immediately and charged the hyaenas, who promptly retreated. Hyaenas have been seen followed rhinoceros with calves older than four months, sometimes approaching extremely close to the calf, who occasionally charged them. In these cases, no serious attempt was made to grab the calf. If the calf loses its mother it is probably vulnerable to predation to a considerably older age.

RECRUITMENT RATES

The composition of the two rhinoceros populations by sex and age is shown in Table 5, and it is apparent that the two are similar in structure. The cow-calf ratio is 1: 0.72 at Ngorongoro and 1: 0.79 at Olduvai. The number of rhinoceros recorded at Olduvai is believed to be the total population, but

TABLE 5

Structure of two black rhinoceros populations by sex and age at Ngorongoro Caldera and Olduvai Gorge, 1966

Sex and age	Ngorongoro		Olduvai	
	Total	% of total population	Total	% of total population
Adult ♂♂	37	34.2	22	30.0
Adult ♀♀	29	26.8	19	25.8
Imm. ♂♂	9	8.3	10	13.4
Imm. ♀♀	12	11.1	8	10.8
Calves ♂♂	10	9.4	9	12.0
Calves ♀♀	8	7.4	6	8.0
Calves (sex unknown)	3	2.8	0	0.0
Total:	108*	100.0	74*	100.0
Cow: calf ratio	100 : 72		100 : 79	

* Includes the 1966 recruitment to the population.

although a substantial number were observed in the caldera of Ngorongoro (108 individuals), I do not consider that all rhinoceros which live there have been recorded.

In order to obtain information on recruitment rates I photographed eight calves of known ages each month over a two-year period. In three cases the birthday of the calf was known to within five days. Photographs were taken of the calf, both in profile and full face, alongside the mother. Growth was observed by relating the shoulder height of the calf to the estimated shoulder height, and to other parts of the anatomy, of the female. In nine cases animals were immobilized to obtain measurements of adult females and their calves. The development of the anterior and posterior horns of the calf was also examined.

Using these photographs of "known-age" calves, it was possible to estimate the age of calves which had been photographed during the early part of the study period. If a calf was less than one year when the original photograph was taken, I believe it is possible to estimate its correct age to within two months. In the second year it is more difficult as growth does not appear to be as regular as in the first year, but in most cases it is relatively easy to estimate the year of birth.

Thus it was possible to establish minimum recruitment rates for four years (1963-1966) for the two populations, by establishing the probable age of calves and by using data recorded from new births. The recruitment data at Olduvai is collected from the total population, and is almost identical with the results obtained at Ngorongoro. Factors affecting recruitment rates are considered below.

a. Age at maturity

No precise data on this factor has been collected in the wild, but there are two fairly accurate zoo records. One is reproduced with the kind permission of Mr. S. Yamamoto, Secretary of the Kobe Oji Zoological Society, Japan. A male black rhinoceros was born in the Kobe Oji Zoo in November 1963. Both parents arrived at the zoo in 1959, the estimated age of the female then being four years and that of the male three years. The pair mated on 4th August, 1962 and produced a calf on 16th November, 1963. If the ages of the parents were estimated correctly in 1959, the male was six years old, and the female seven years old, at the time of their first mating.

Dittrich (1966) presents data on the parents of a black rhinoceros born in the Hanover Zoo in 1965. In 1959 the female was three years old and the male one year. At the end of 1962 the female (now six) developed oestrus periods every month. For sometime the male took no interest in her, but on 10th March, 1964, when the male had reached his sixth year, copulation occurred.

b. Gestation period

There is considerable reference in the literature to the gestation period of the black rhinoceros; records vary from 450-545 days (c.15-18 months). Ulmer (1958) gives 450-480 days. Two calves produced in the Kobe Oji Zoo had gestation periods of 470 and 462 days. A record from the Hanover Zoo in Germany gives 469 days (Dittrich 1966). I have two records from the population at Ngorongoro. One female was in receptive oestrus on 7th April, 1965 and produced a calf during the last week of June 1966, giving a gestation period of approximately 446 days. The other animal was mated on 17th September, 1965 and produced a calf sometime during the period 5-9th January, 1967, giving a gestation period of approximately 478 days.

c. Interval between calves

The interval between calves in this species also varies. A pair of black rhinoceros in the Chicago Zoo produced a calf on 7th October, 1941 and another calf on 19th September, 1944. Two calves born to the same female in the Kobe Oji Zoo in Japan were born exactly 24 months apart. I have several records from the population at Ngorongoro, established by using the series of "known-age" photographs, together with records of new calves born to the

same mother. Table 6 shows that one female (no. 2) gave birth to calves in August, 1963 and September, 1965 (a 25-month interval); no. 4 had calves in September, 1963 and January, 1966 (a 28-month interval), and no. 8 in November, 1963 and April, 1966 (a 29-month interval). The available evidence suggests, therefore, that a normal healthy female could be expected to produce a calf approximately every 27 months.

d. Lactation and the onset of oestrus

After parturition the onset of oestrus followed by conception also varies considerably. Dittrich (1966, pers. comm.) reports that the female which gave birth to the calf in Hanover Zoo (quoted above) developed an oestrus period 20 days after parturition. Because the male was denied access to her, she continued to develop oestrus periods every 25-30 days, but was successfully bred in June, 1966.

The onset of oestrus does not appear to be closely associated with reduced lactation in the species. One female in Ngorongoro was still lactating 17.5 months after parturition, although working on the assumption that the appearance of a moist vaginal mucosa and a swollen vulva is a good diagnostic character of oestrus (Asdell, 1964) she developed regular oestrus cycles three months after parturition.

The female may apparently develop regular oestrus cycles within a few weeks of parturition but the calving-conception interval is relatively long. Assuming that most cows can produce a calf every 27 months (section c, above) and that the gestation period is 15-16 months, it is apparent that successful conception does not occur until about a year after parturition, despite the cow's regular oestrus cycles and apparent receptiveness to the bull.

It seems likely that the ovarian activity of the black rhinoceros resembles other species in the Perissodactyla. King (1965) reports the occurrence of oestrus cycles soon after parturition in two species of zebra (*Equus burchelli* Gray and *E. grevyi* Oustalet), but the foaling-conception interval varied from 2-24 weeks in some *E. burchelli*. The ovarian activity of the rhinoceros may resemble the horse, where the ovary is not suppressed by lactation but continues to cycle regularly after the first post-partum oestrus (King, 1965).

The difference in length of gestation periods and the variations in times of successful conception after parturition, even when the female demonstrates regular oestrus cycles, probably account for the observed differences in intervals between calves. One female in Ngorongoro was observed mating in April, 1964. She had a calf at foot whose age was estimated at approximately one year. She was mated, but not successfully, and was observed being mounted by several bulls one year later in April, 1965. The calf was born in June, 1966 and the interval between successive calves of this particular female was thus 38 months.

The recruitment rates of the two rhinoceros populations are shown in Tables 6 & 7 and are almost identical, being 7.0% at Ngorongoro and 7.2% at Olduvai. As mentioned above it is believed that a normal healthy female can produce a calf approximately every twenty-seven months. If conception occurs within one or two months after parturition it is possible that the interval between calves may be as short as eighteen months. The ratio of calves per year/adult female was 0.25 at Ngorongoro and 0.26 at Olduvai, demonstrating an overall recruitment of one calf per female every four years. This recruitment is relatively low when compared with a calf interval of twenty-seven months postulated for a normal healthy female. Field observations suggest that calf mortality is not high, and it is probable the populations are being controlled by a self regulatory mechanism, such as reduced fertility rates.

Mortality data have been recorded for the two populations by the collection of skulls. The rhinoceros is a species that lends itself to relatively easy appraisal of mortality rates of the older age classes as the skull does not deteriorate for some years, being fairly resistant to the normal effect of

TABLE 6

Recruitment of calves to the 29 adult females present at Ngorongoro 1963 - 1966

Adult female	1963	1964	1965	1966
1	—	♂	—	—
2	♀ (Aug.)	—	♀ (Sept.)	—
3	♀	—	—	c*
4	♀ (Sept.)	—	—	♂ (Jan.)
5	♂	—	—	♂ (Jun.)
6	—	—	♀ (Jun.)	—
7	—	—	♂ (Feb.)	—
8	♀ (Nov.)	—	—	♂ (April)
9	♂	—	—	c*
10	—	♂	—	—
11	—	♂	—	—
12	—	c*	—	—
13	♂	—	♀ (Oct.)	—
14	—	♀	—	—
15	—	♀	—	—
16	—	♀	—	—
17	—	♂	—	—
18	♀	—	—	c*
19	—	—	♀	—
20	—	—	♂	—
21	—	—	—	c*
22	—	—	—	—
23	—	—	—	—
24	—	—	—	—
25	—	—	—	—
26	—	—	—	—
27	—	—	—	—
28	—	—	—	—
29	—	—	—	—
Total:	8	8	6	7

Mean no. calves per year - 7.2.
Ratio calves per year/adult females - 7.2 : 29 = 0.25.
Ratio of calves per year/all adults - 7.2 : 66 = 0.11.
Ratio of calves per year/whole population - 7.0%.

c* — sex of calf unknown.
Dates in parentheses = month of birth where known.

TABLE 7

Recruitment of calves to the 19 adult females at Olduvai Gorge, 1962 - 1966

Adult female	1962*	1963	1964	1965	1966
1		♂	—	—	♂
2		♂	—	♂ (Dec).	—
3		—	♂	—	—
4		♀	—	—	♀ (Aug.)
5		♀	—	—	—
6		—	—	♀ (April)	—
7	♀	—	—	♂ (Sept.)	—
8		—	♀	—	♀ (Jan.)
9		♂	—	—	♂ (Feb.)
10		—	♂ (died?)	—	—
11	♂	—	—	—	—
12		—	♀	—	—
13		—	—	♀	—
14		—	—	♂	—
15		—	—	♂	—
16		—	♂	—	—
17		—	—	—	—
18		—	—	—	—
19		—	—	—	—
Total:		5	5	6	4

Mean no. calves per pear - 5.0

Ratio of calves per year/adult females - 5:19 = 0.26.

Ratio of calves per year/all adults - 5:41 = 0.12.

Ratio of calves per year/whole population - 7.2%.

* The actual recruitment during this year is unknown. The two individuals shown in 1962 were considered born in this year, from photographic measurements of the individuals taken during 1964.

Dates in parentheses = month of birth where known.

scavengers. It is possible to estimate the year of death of the rhinoceros by examination of the condition of the skull, but the maxilla and mandible deteriorate considerably faster in a marsh environment than in a dry, arid one. I collected two skulls from animals whose dates of death were known. One had been shot five years before in grassland and the skull was in excellent condition; the other was shot in a marsh 11 years before collection. The skull, lying under mud, had deteriorated considerably although the pelvic girdle (situated on dry land) was intact.

If it is assumed that neither adult nor immature skulls deteriorate beyond re-

cognition for at least five years then the sample collection of skulls made in the two areas gives an estimate of the mortality of the populations during the study period. From this it appears that, at present, the mortality rates do not exceed the observed recruitment rates, and the populations are probably stable, if not increasing. It is possible that mortality from heavy poaching in the past (21 rhinoceros were speared in the Ngorongoro Conservation Area during 1960, of which eight were killed in or near the caldera) may have exceeded the recruitment rate, but the infliction of severe penalties on offenders now appears to keep the problem to a minimum. The future of the species in the Ngorongoro Conservation Area appears to be good.

ACKNOWLEDGEMENTS

I should like to thank Mr. H. A. Fosbrooke, formerly Conservator of the Ngorongoro Conservation Area, and his successor Mr. S. ole Saibull for their continuous encouragement and support in the work.

A special word of thanks is due to Mr. G. Frame who helped considerably in the field work during the terminal part of the study period, and to Mr. Richard Leakey for his splendid hospitality at Olduvai.

REFERENCES

ASDELL, S. A. (1964). Patterns of mammalian reproduction. 2nd Edition. *Comstock Publishing Company Inc.*, Cornell University Press, Ithaca, New York. 670 pp.

DITTRICH, L. (1966). Geburt eines Spitzmaulnashorns im Zoo Hannover. *Zoologischen Garten, Hannover.*

GODDARD, J. (1966). Mating and courtship of the black rhinoceros. *E. Afr. Wildl. J.*, 4: 69-75.

KING, J. M. (1965). A field guide to the reproduction of the Grant's zebra and Grevy's zebra. *E. Afr. Wildl. J.*, 3 : 99-117.

RITCHIE, A. T. A. (1963). The black rhinoceros (*Diceros bicornis* L.). *E. Afr. Wildl. J.*, 1 : 54-62.

ULMER, F. A. (1958). On breeding rhinoceroses. *America's First Zoo*, 10 (3) : 3-6.

Author's address: J. Goddard, c/o P.O. Box 14, Voi, Kenya.
(Received for publication December, 1966)