Mammalia depicta

Herausgeber: Wolf Herre, Kiel · Manfred Röhrs, Hannover

R. Schenkel · L. Schenkel-Hulliger

Ecology and Behaviour of the Black Rhinoceros

(Diceros Bicornis L.)

A Field Study

Verlag Paul Parey

Among many other animals, man also endangers the five surviving rhino species. Only within the last decades, efforts have been made to safeguard the rhinos from extinction and only recently to study their way of life.

The present monograph deals with the black rhinoceros. It describes the relevant qualities of its habitat, its ecological situation in a restricted area of Tsavo National Park East in Kenya, and more generally its behaviour and social life.

As rhinos are rather solitary animals, the degree of intraspecific intolerance and aggression, and the communication systems providing for the continuity of the population are of special interest. Rhinos show a remarkable degree of adaptability; depending on their habitat, populations live in a more sedentary or more nomadic way. As is shown by the authors, the rhino's reactions are not purely innate. Some are formed by tradition within the local population, i.e. transferred from mother to calf. This is especially obvious for reactions of rhinos to man.

Die fünf rezenten Nashornarten gehören zu den interessantesten Säugetieren des Erdballs; in ihrem Fortbestand sind sie gefährdet. Um wirkungsvolle Maßnahmen zur Rettung der Arten einleiten zu können, ist eine genaue Kenntnis ihrer Biologie unentbehrlich, die aber im Hinblick auf die Eigenarten dieser Tiere auch allgemeines Interesse verdient. Die vorliegende Veröffentlichung befaßt sich mit dem Schwarzen Nashorn Afrikas. Durch Klärung der Lebensansprüche dieser Art will sie deren Erhaltung fördern.

Um die besonderen Ansprüche des Schwarzen Nashorns an den Lebensraum beurteilen zu können, wird der Biotop einer Population eingehend untersucht. Es folgt eine sorgfältige Analyse des arteigenen Verhaltens. Dabei ergeben sich Tatsachen von allgemeiner Bedeutung. Das Schwarze Nashorn lebt wenig sozial; Fragen nach Ursachen und Umfang der innerartlichen Intoleranz waren zu klären, Probleme der innerartlichen Kommunikation wurden aktuell. Je nach Biotop haben Nashornindividuen eine mehr seßhafte oder stärker nomadische Lebensweise, es galt die Zusammenhänge aufzuklären. Auch in anderen Besonderheiten, so in der Reaktion auf den Menschen, zeichneten sich lokale Traditionen ab. Diese Tatsachen waren Anlaß, der Plastizität im Verhalten des Schwarzen Nashorns besondere Beachtung zu schenken. Ein vielseitiges Bild vom Leben des Schwarzen Nashorns konnte entworfen werden, das Hinweise für einen erfolgversprechenden Naturschutz gibt.

ECOLOGY AND BEHAVIOUR OF THE BLACK RHINOCEROS (DICEROS BICORNIS L.)

A Field Study

By

PROF. DR. RUDOLF SCHENKEL

Zoologische Anstalt der Universität Basel

and

DR. LOTTE SCHENKEL-HULLIGER

26 Figures and 7 Tables

1969

VERLAG PAUL PAREY · HAMBURG UND BERLIN

LANDWIRTSCHAFT · VETERINÄRMEDIZIN · GARTENBAU · FORSTWESEN · JAGD UND FISCHEREI

HAMBURG 1 · SPITALERSTRASSE 12

MAMMALIA DEPICTA

Eine Schriftenreihe, herausgegeben von Prof. Dr. Dr. h.c. WOLF HERRE, Kiel, Neue Universität und Prof. Dr. MANFRED RÖHRS, Zoologisches Institut der Tierärztlichen Hochschule Hannover

Dedicated to
Prof. RUDOLF GEIGY, Basel
who opened the way to Africa for us

FOREWORD

In cultivating the soil, man has waged a relentless war against the forest, while the cleared areas have, in turn, attracted many species of large herbivores adapted to open country or a transitional habitat between savannah and forest proper. From the ensuing ecological conflict man has emerged superior to these mammals. Human settlement has spread continuously whereas many of the larger herbivores have vanished or are on the verge of extinction. Such is the position of the three Asian and although less critical of the two African species. Besides ecological competition, big game hunting and organised poaching to meet the demand for trophies and imaginary aphrodisiacs have aggravated the situation. Only strict protection will save the rhino from extinction and, as the animals will, at best, be tolerated in restricted areas, careful management is essential. The impulse to begin this study originated partly from management problems. One of the most important strongholds of the black rhinoceros, Tsavo National Park East, Kenya, had suffered heavy losses in 1960/61, two years of heavy drought. The scarcity of water effected the animals directly and also indirectly in causing severe food shortage. Moreover the situation was aggravated by the impact of an increasing elephant population. Over the last 10 to 15 years the elephant has gradually destroyed important components of the vegetation, mainly Commiphora and Acacia trees, Sanseveria and bush thickets. Concurrently with bush fires, it has in large parts of the park, radically altered the whole vegetation: former bush country has become dry grassland. How does the rhino population react to the changes that are constantly going on in its habitat?

The problem called for an ecological study of the local rhino population. At the same time it was felt that the behaviour and social attributes of the black rhino were only superficially known. Therefore the authors decided to study both the ecology and behaviour of the species.

The investigation was carried out between January 1963 and October 1966. During the greater part of this time, the authors were members of the staff of the University College Nairobi, delegated by the Swiss Technical Aid. The observations were made in Amboseli Game Reserve during several short periods in 1963; in Tsavo National Park East in 1964 (during the months of June, July, August and for short periods in September and October), in 1965 (for 1 week in March and during the months of July and August) and in 1966 (for three weeks in September and October). In addition rhinos were observed during visits to several National Parks and Game Reserves in East Africa.

During this time we were given support and encouragement by many people to whom we wish to express our gratitude. First of all we want to thank PROF. DR. RUDOLF GEIGY, Schweiz. Tropeninstitut Basel, who launched us on our mission to East Africa. We are also very grateful to DAVID SHELDRICK, Game Warden in Tsavo National Park East, whose long experience in the park enabled him to contribute excellent suggestions and helpful criticism and who, together with his wife DAPHNE, offered us generous hospitality. We also thank PETER JENKINS, Assistant Game Warden in Tsavo East, and his wife SARAH who helped us on many occasions. In our field work we were assisted by CORPORAL KILUNDA and his younger colleagues to whom we also owe gratitude. Our work was made possible by the authorities of the Kenya National Parks who supplied helpers, camping equipment and a vehicle during the

course of the field observations. We are grateful to COLONEL M. COWIE, former Director of Kenya National Parks, to MR. OLINDO, Director of Kenya National Parks, and to DR. M. HYDER, Chairman of the Trustees of the Kenya National Parks for their interest in our work. Helicopters were made available to the Kenya National Parks for the flights by the British Navy in July, 1964 and 1965 and by the R.A.F. in September, 1964.

We are grateful for the interest shown by PROF. D. KETTLE and colleagues in the Department of Zoology, University College Nairobi. Our thanks are also due to DR. J. SALE for providing a telescope, to DR. A. AGNEW for assisting in the determination of the food plants and to DR. J. BERGER and DR. JANE WALKER for identifying parasites. We are most grateful to TEDA AND PROF. D. SEARS, Adelaide for reviewing the manuscript.

The manuscript was prepared with the support of the Schweiz. Nationalfonds (Nr. 3827).

CONTENTS

ECOLOGY

I. Habitat

A. Topography

The black rhinoceros occurs in Tsavo National Park East wherever permanent water is available to the animal. One finds it (Fig. 1) in the plains south of Galana River – especially near the river –; near Aruba Lodge and Voi River; on the basement rock hills from Voi Entrance to Mudanda Rock and Tsavo River and their surroundings; on the Yatta Plateau with its adjacent plains.

All these areas are suitable for the species wherever there is abundant and varied bush vegetation forming occasional thickets.

B. Ecological requirements

1. Permanent water supply

During the excessively dry years 1960 and 1961 Athi, Tsavo, and Galana River, the Upper Tiva River, and Wamuntumia Spring were the only waters which did not dry out completely. Aruba Dam was reduced to a muddy puddle and the Tiva River dried out in its lower reaches.

In years with an average rainfall, e.g. 1964 and 1965, in addition to these permanent water sources, several smaller streams on both sides of the Galana and the Tsavo River from Mtito Andei to Sobo, and many small springs in the Yatta Plateau from the northern park boundary to Lugard Falls contain water also during the dry season. A number of other rivers and pools including Voi River dry out regularly.

2. Food plants

The black rhinoceros is a browser and lives on a variety of bushes and shrubs. Some of the most important food plants on which the rhino feeds were collected in the Galana-Yatta Region in 1964 and 1965.

Single animals were followed along their feeding routes and their feeding habits observed. Food plants were then collected immediately or noted as such. Also samples of plants were included which showed typical signs of rhino feeding (see Fig. 2).

They are listed by their frequency of occurrence and feeding by rhinos (Table I). Rhinos feed most extensively on the plants, listed under A., which occur frequently in the observation area. On a large number of other bushes and shrubs they feed only occasionally, either because these are too rare to be a main constituent of their diet, or because they only seem to attract rhinos temporarily. A number of these plants were collected and are listed under B. in Table I. It should also be mentioned that some frequently occurring bush and shrub species are not eaten by rhinos at all (C. in Table I).

Table 1

Food plants of the black rhinoceros collected in the Galana-Yatta Region as identified by the E. A. Herbarium, Nairobi

Name	Family	Type	Eaten by elephants also
A. Plants that occur frequently in the area and are eaten preferably			
Aerva persica (Brum.F.) Merr.	Amaranthaceae	herb	—
Bauhinia taitensis Taub.	Caesalpiniaceae	bush	+
Blepharia sp.	Acanthaceae	woody herb	—
Caucanthus albidus Nied.	Malpighiaceae	shrub	—
Cordia ovalis R.Br.	Boraginaceae	shrub	—
Cordia rothii Roem. & Schult.	,,	shrub	—
Ehretia titensis Guerka	,,	shrub	—
Sericocomopsis pallida Sp. Moore	Amaranthaceae	shrub	+
Sericocomopsis hildebrandtii (C.B.Cl.) Schinz	,,	shrub	—
Suaeda monoica Forsk ex J.F.Gmel	Chenopodiaceae	shrub	+
B. Plants that occur only occasionally a. and are eaten extensively			
Acacia tortilis (Forsk.) Hayne	Mimosaceae	tree or shrub	+
Becium sp.	Labiatae	herb	—
Caesalpina trothae Harms	Caesalpinaceae	shrub	—
Commiphora sp.	Burseraceae	tree	(+ ?)
Crotalaria sp.aff.C. pallida Ait.	Papilionaceae	herb	—
Dirichletia glaucescens Hiern	Rubiaceae	bush	+
Grewia lilacina K. Schum.	Tiliaceae	shrub	+
Grewia villosa Willd.	,,	shrub	+
Hermannia exappendiculata (Mast.) K. Schum.	Sterculiaceae	woody herb	—
Indigofera vohemarensis Baill.	Papilionaceae	woody herb	—
Secamone stenophylla N.E.Br.	Asclepiadaceae	woody climber	—
Triumfetta flavescens (Lam.) Benth.	Tiliaceae	woody herb	—
b. and are eaten occasionally			
Abutilon sp.	Malvaceae	shrub	(+ ?)
Anisotes parvifolius Oliv.	Acanthaceae	shrub	—
Asparagus asiaticus L.	Liliaceae	climber	—
Asparagus falcatus L.	,,	,,	—
Barleria acanthoides Vahl	Acanthaceae	shrub	—
Barleria stuhlmanii Lindau	,,	shrub	—
Barleria taitensis S. Moore	,,	shrub	—
Boscia angustifolia A. Rich.	Capparidaceae	tree	—
Cadaba farinosa Forsk.	,,	shrub	—
Cadaba glandulosa Forsk.	,,	shrub	—
Combretum aculeatum Vent.	Combretaceae	shrub or climber	—
Combretum exalatum Engl.	,,	shrub	—
Crotalaria drummondii Milne-Redhead	Papilionaceae	shrub	—
Disperma kilimandscharica (Lindau) C.B.Cl.	Acanthaceae	shrub	—
Dyschoriste depressa Need	,,	shrub	—

Continuation p. 15

Continuation Table 1

Name	Family	Type	Eaten by elephants also
Ecbolium revolutum C.B.Cl.	Acanthaceae	shrub	—
Ecbolium subcordatum C.B.Cl.	,,	shrub	—
Euphorbia jatropoides Pax	Euphorbiaceae	shrub	—
Euphorbia polyantha Pax	,,	shrub	—
Euphorbia spinescens Pax	,,	shrub	—
Haplocoelum foliolosum (Hiern) Bullock	Sapindaceae	tree	—
Helichrysum glumaceum DC.	Compositae	woody herb	—
Hibiscus micranthus L.F.	Malvaceae	herb	—
Hildebrandtia obcordata Sp. Moore	Convolvulaceae	shrub	—
Indigofera spinosa Forsk.	Papilionaceae	woody herb	—
Ipomoea jaegeri Pilg.	Convolvulaceae	woody herb	—
Kigelia africana (Lam.) Benth.	Bignoniaceae	tree	—
Lawsonia inermis L.	Lythraceae	shrub	—
Lepidagathis scariosa Nees	Acanthaceae	weak shrub	—
Marua subcordata (Gilg) De Wolf	Capparidaceae	low shrub	—
Moringa sp.	Moringaceae	shrub	—
Monechma debile (Forsk.) Nees	Acanthaceae	herb	—
Ormocarpum kirkii S. Moore	Papilionaceae	shrub or tree	—
Pavonia patens (Andr.) Chiov.	Malvaceae	woody herb	—
Pavonia zeylanica (Hochst.) Schauer	,,	annual woody herb	—
Premna resinosa (Hochst.) Schauer	Verbenaceae	shrub	—
Psychotria nairobiensis Brem.	Rubiaceae	shrub	—
Pupalia lappacea (L.) Juss	Amaranthaceae	herb	+
Seddera hirsuta Hall. f.	Convolvulaceae	shrub	—
Solanum incanum L.	Solanaceae	spiny herb	—
Strophanthus mirabilis Gilg	Apocynaceae	shrub	—
Strychnos sp.	Loganiaceae	shrub or tree	—
Stylosanthes fruticosa (Retz.) Alston	Papilionaceae	shrub	—
Talinum portulacifolium (Forsk.) Asch. & Schweinf.	Portulaciaceae	fleshy herb shrubby	—
Tephrosia noctiflora oj. ex Bak.	Papilionaceae	woody herb	(+)
Tinnea aethiopica Kotschy & Peyr.	Labiatae	shrub	—
Xeromphis sp.	Rubiaceae	shrub or tree	—
C. Plants occurring frequently in the area, but not eaten by rhino			
Boscia coriacea Pax	Capparidaceae	tree	
Thylachium thomasii Gilg	,,	tree	

3. Vegetation cover

The rhinoceros needs sheltering vegetation. In the heat of the day the rhinos often rest and sleep in the shade of a tree or a dense bush. In this way they are protected from the sun's rays and wind, and cannot be detected easily by man – the main enemy of the species. In case of disturbance by man on foot, in a car or an aircraft, rhinos often tend to hide in dense bush after first escaping.

4. *Wallows*

Rhinos visit muddy wallows regularly whenever they have the opportunity. Only places with a solid base and a comparatively shallow sheet of mud and water are suitable for them. In most parts of Tsavo National Park East this possibility does not

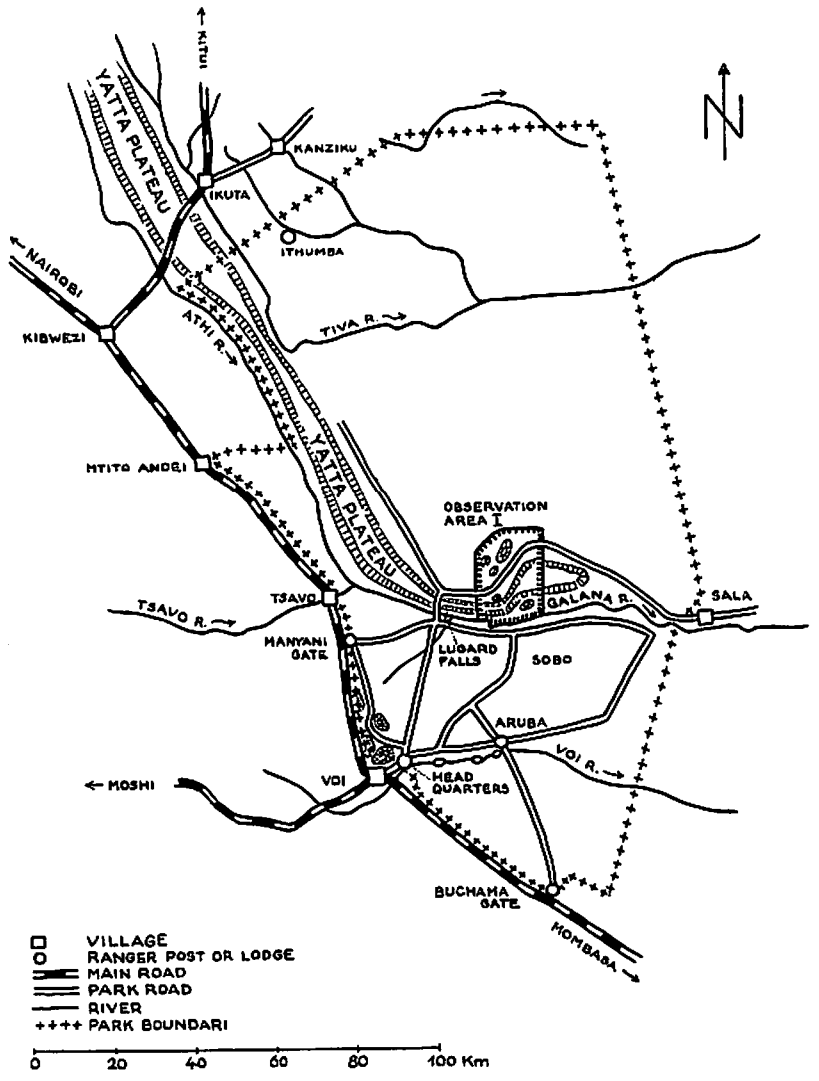

Figure 1. Map of Tsavo National Park East with observation area I.

exist during the dry season. Then the rhinos wallow in dusty or very fine-grained soil, mostly provided by termite hills.

Mud wallowing does not exclude dust wallowing. The black rhinoceros sometimes rests and sleeps in water, as do the Indian and the squarelipped rhinos, but in Tsavo East this is impossible during the greater part of the year. Then they often lie in dust wallows for several hours a day. A prolonged bath may have a temperature regulating effect, but wallowing in mud for a short time and lying or wallowing in dusty soil must have other functions. Presumably wallowing has a favourable effect on the skin condition and protects against ectoparasites, mainly biting flies, by covering the skin with a film of soil or dust. Parts of the body which are not wallowed frequently e.g. the saddle region, are those most attacked by flies, while other parts are covered with a sheet of soft mud or fine grain soil (see Fig. 8).

C. Impact of the rhinoceros on its habitat

By its activities the rhino changes some aspects of its habitat in a characteristic manner.

1. *Vegetation*

Where a considerable part of the vegetation is eaten by rhino, a special pattern of bush and shrub vegetation develops which may be called "brush pattern". The branches of the bush are cut down by the rhino more or less evenly to a level between 10 cm and 1 mtr. Lateral branches are sometimes cut lower than those in the centre. When new shoots grow out of the older branches, they are cut off again (Fig. 2).

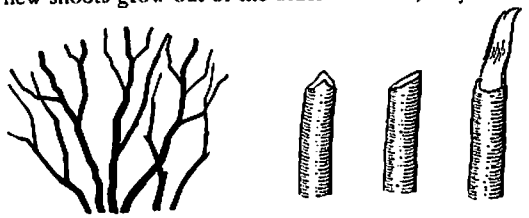

Figure 2. Effect of feeding by the rhino on the structure of bush ("brush" pattern).

Most twigs are cut off neatly by the premolars; in some bush species with tough branches (e.g. Bauhinia taitensis) the severed twigs often end in a wooden spike, the result of biting, bending down and twisting at the same time. It should be mentioned here that the "brush pattern" of the bush and shrub vegetation is never due to browsing by elephants. When browsing on bush plants, elephants strip the leaves and the ends of the twigs off with their trunks, or break smaller branches by bending them over a tusk. Sometimes, when a branch is attached very low, an elephant may seize it with the trunk and break it off by stepping on it with a forefoot.

2. *Tracks*

Another feature characteristic of rhino country is a system of tracks. Within the system there are tracks of different appearance and different function. Large paths, used by elephants and rhinos, extend over several miles from feeding areas to watering places. These tracks fit into the topography in a remarkable way. They climb up the Yatta Plateau through little valleys and gaps by the easiest route (Fig. 3). They follow the course of small valleys in the plateau taking advantage of even minute features of the terrain, such as flat strips and the least rocky surfaces.

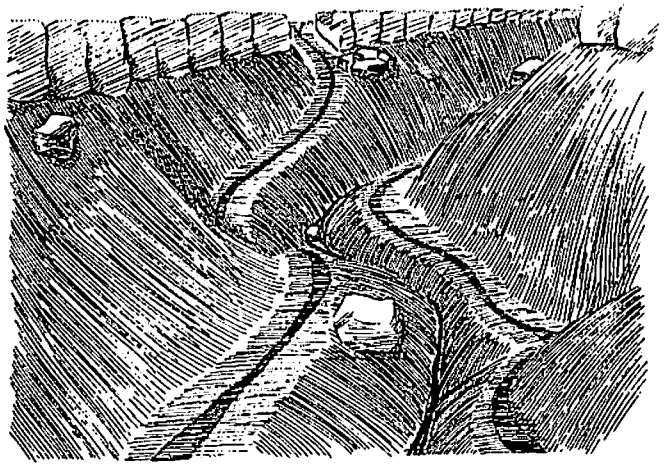

Figure 3. Main tracks as easiest routes.

South of Galana some of these tracks lead along the valleys as long as their bottoms are flat (Fig. 4). Most of them however run on the flat ridges.

All the large tracks are connections resulting from a strong desire to get to water or to remote feeding areas quickly, and are smooth, requiring minimum effort to reach their respective aims. We use the term "main tracks" for this type of track. They have no vegetation cover left and most of them are permanently used and maintained mainly by elephants, but also by rhinos. There are of course also tracks in the area which are regularly used by rhinos but not by elephants. They are comparatively narrow and neat and have many minor bends bypassing small trees or even bush plants. Other mammals also make use of main tracks, without having a major impact on them, e.g. other ungulates (buffalo, zebra), carnivores, baboon, porcupine. Elephants and rhinos often move to and from water over several miles without feeding. When on the move, elephant family-units often follow these tracks in single file. Rhinos, singly or in pairs one behind the other, walk either carrying the head in normal fashion or with their noses down sniffing scent components of the track. Rhinos often walk steadily at a speed of 3–5 kilometers per hour along the main track for $^1/_2$ hour or longer. Then they may slow down and feed occasionally, still keeping to the main direction. Under these circumstances they usually leave the main track and follow secondary tracks more or less parallel to the main track, which form a "stretched" network along the latter. This occurs most often in places where the main track does not meet any topographical obstacles which might have a canalising effect. We call these secondary tracks "moving-feeding tracks" (Fig. 5).

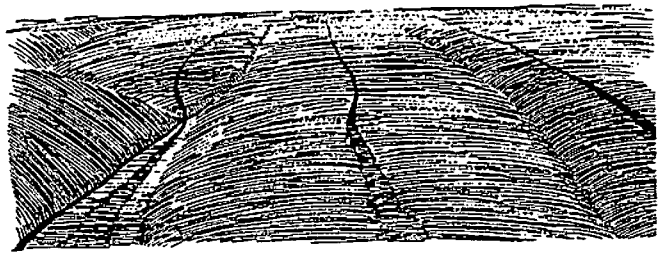

Figure 4. Main tracks in relationship to valleys.

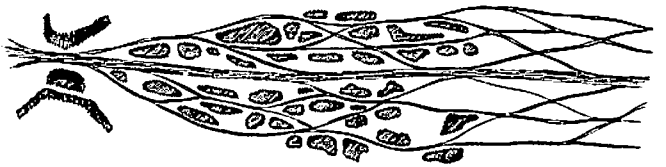

Figure 5. Moving-feeding tracks accompanying a main track.

A system of these tracks can occasionally occur without a main track. The latter can "split up" completely into moving-feeding tracks, e.g. where a strip of healthy bush vegetation extends in the direction along a valley on the banks of a seasonally dry river bed (Fig. 6).

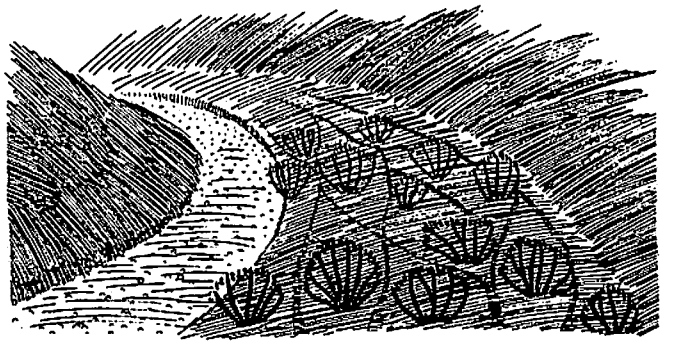

Figure 6. Pattern of moving-feeding tracks along a river bed.

High intensity browsing takes place in the feeding areas proper. Feeding areas are found at any distance up to 20 kilometers and even more from permanent water. Rhinos often interrupt their progress to the water and feed intensely in areas near the main track.

When feeding, the rhino stands near a bush, cuts a branch and chews it. Then it cuts another branch and so on. Then it slowly moves on to the next bush. This type of slow locomotion results in a network of "feeding tracks", which pass between bushes in every direction. Feeding tracks are, in contrast to the main tracks and to most of the moving-feeding tracks, still covered with some vegetation, e.g. with grass and very short shrubs obviously trampled by the walking rhinos.

Between these three types of tracks there are of course also intermediate forms. It is the different proportion between two "appetites" of the animal – the drive towards a distant aim, water or a remote feeding area, and the tendency to endulge in feeding on the spot, which shapes the components of the track system.

3. Dung heaps and scraping places

Along all these kinds of tracks the rhinos deposit their dung, very often in places which have been used previously – often many times – by different individuals. After defeca-

tion on a dung place, the animal breaks the dung balls into pieces by scraping with its hindlegs, and in this way produces two flat parallel ditches. The social function of this modus of defecation will be discussed in a later chapter.

Large dung heaps are often found near watering places, along the main tracks, in places where they branch off, and in feeding areas. In many cases a small tree or a bush forms the centre of the heap. Some rhino "lavatories" are used from one side only, others from two or more sides (Fig. 7).

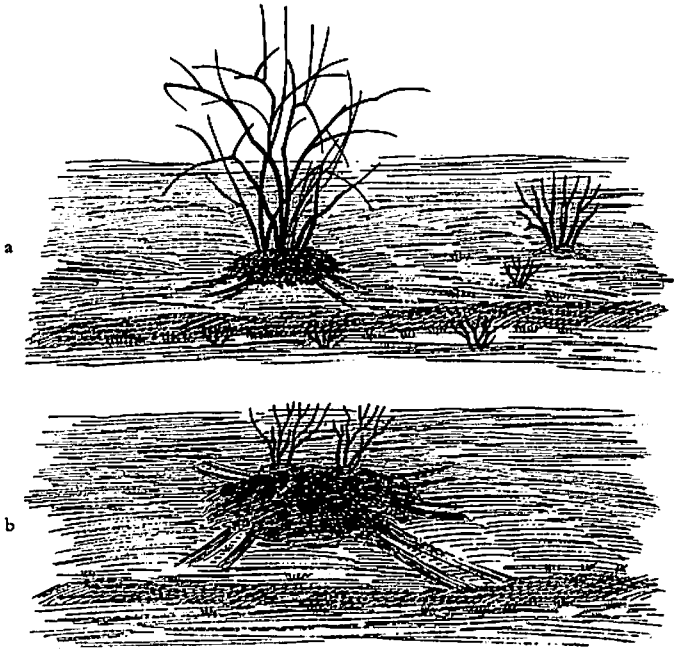

Figure 7. Lavatory used a. from two, b. from more sides.

Rhino dung is easy to identify; its main contents are short pieces of twigs about 1 to 3 cm long, without bark, sometimes split longitudinally. It also has a characteristic scent.

Rhino bulls sometimes scrape without defecation, and in certain situations they may scrape and trample over a small bush, knock it down with the first horn and completely smash it. Traces of this activity are often found near main tracks.

4. Urination

The adult male rhino normally squirts its urine on to bushes or shrubs in a ritualized manner. When the urine droplets dry, they form small white spots all over the plants. No deleterious effect on the plant was observed.

Females normally urinate in a non-ritualized manner, i.e. the urine is released in a continuous, pulsating stream. But when on heat they squirt urine frequently in small quantities. Sometimes females urinate in a ritualized manner without showing other signs of rutting condition.

5. Dry wallows

The dry wallowing and sleeping places which have already been mentioned are "developed" by rhinos themselves, usually from termite hills.

When in optimal condition the wallow is covered by a sheet of about 10 cm of very loose fine-grained soil. The centre of the wallow has a slight depression and is surrounded by a low rim of loose soil. When the place is well developed, it is used by many different rhinos. Sometimes signs of competition over a wallow could be observed.

After a certain time, which according to our observations may be a few months, the place is no more used. Several factors contribute to the deterioriation of a wallow, e.g. wind carries the fine soil away, or rain washes it off during the wet season. In our observation area none of the 3–4 wallows which were most often used in July/August 1964 were still in use in the following year (March and July/August 1965). About an equal number of new wallows were developed and used in 1965.

Wallows are to be found in feeding zones and near main or secondary tracks and on the banks of the river. Rhinos often visit these places after their morning feeding period, or they interrupt a trip to the water in order to wallow. Mothers with babies and calves were observed to suckle on a wallow. Mating also may occur there.

6. Watering places

In the observation area rhino and elephant tracks converge from a large area towards one main watering place at the Sobo bend of the Galana River (see Fig. 11). One important reason for the convergence of main tracks in this area lies in the topography of the watering place. The water is easily accessible over a distance of more than 100 mtrs, the banks of the river are only partially rocky, the terrain is relatively open, and a newly arriving rhino is easily seen. In addition the topography of the river bend and its surroundings canalizes the wind towards the watering place, so that it is difficult to approach it without causing alarm by scent.

It seems that there is another reason for the congregation of rhinos from a large area to one watering place: rhinos have a tendency to meet there. The social significance of such a meeting place will be discussed later.

At watering places which are used by many rhinos and also by elephants, the banks of the river are densely marked with footprints and there is hardly any vegetation left. Large rhino dung heaps align along the main tracks near the river.

Summary

The most obvious impact of the black rhinoceros on its habitat is the special brush pattern of the vegetation caused by browsing. The different elements of the track system are conspicuous. But, wherever feeding tracks cover the soil densely, forming a real network, wherever the main tracks look like small roads and are accompanied by a whole system of more or less parallel moving-feeding tracks, this is due mainly to simultaneous elephant activity.

Rhino lavatories are easy to detect even if they have not been used over several months; however, they do not seem to affect the habitat in any important way. Urination, scraping and the occasional smashing of small bushes also do not leave long lasting traces.

II. Relationship between rhinos and other vertebrate species, including man

A. Enemies

1. Rhino and predators

In general, rhinos are not exposed to predation. Lions have been known in a few exceptional cases to attack and kill a rhino. We have observed three subadult lions stalk an adult male rhino from two sides in a more or less playful manner. The rhino lifted its head, walked in a slightly aggressive way towards one lion, then turned towards the other. The lions withdrew when the rhino was within a few meters. The lion obviously does not endanger the species; as with other predators, he prefers to kill with a minimum of effort and risk. However, sick rhinos or calves not sufficiently protected by their mothers may occasionally be attacked by lions or even by hyaenas. In August 1964 we found a sick rhino bull near Galana River. The animal was shot and on closer examination of the dead animal we saw tooth marks in his anal region. The skin of the penis was bitten off, the distal part of the corpus callosum and the urethra formed two separate bodies. Apparently the helpless animal had been attacked by hyaenas. But after considering all the evidence we conclude that the species does not suffer from pressure by predation; it is by no means a limiting factor on a rhino population. Correspondingly, rhinos show no fear of predators and have not developed techniques for their detection or avoidance.

2. Rhino and man

As the black rhinoceros has not developed organs and techniques for the detection of a potential predator from a safe distance, it is extremely vulnerable to man. The rhinoceros has very poor eyesight. Even when optically stimulated, it is usually not alarmed. A rhino may see a moving man within 50 mtrs., look at him and listen, but when he moves away, it soon loses interest. When a man or a car is in sight, but motionless, a rhino will show no interest, unless it is within a distance of about 20 to 30 meters.

The acoustic perception of the rhino is well developed. When feeding or walking, or even when lying, the rhino continously checks the surroundings by rotating its ears. When an observer walks carefully at about 30 to 40 meters from a rhino or even when he remains motionless, he will often notice that one ear of the animal is turned in his direction. But the rhino does not show signs of excitement or of serious alarm. Especially when the observer walks away, the rhino pays hardly any attention. In some cases rhinos walked towards the observer in peaceful curiosity. Generally the reactions of cows to noises produced by man are curiosity – alertness – defense of the calf – flight. Exceptionally self-confident bulls may attack. In most cases however their reactions are between threat and flight.

The responses of the rhino to acoustical and optical stimulation make it very easy to stalk. But in the past, pressure by man has been so heavy that behaviour mechanisms with protective functions had survival value for the species. In fact in regions where they have been hunted or poached extensively rhinos react violently to the presence of man in two situations:

Firstly the perception of human scent immediately elicits intense excitement normally followed by flight, often after a short impulse of defensive threatening with sham-attack and snorting. The reaction is the same when the rhino perceives human scent carried by the wind or when it comes across a fresh scent track of man. It is most likely that the intensity of the reaction is determined by tradition.

Secondly: being unable to detect and identify man by eye or ear, and protected by its olfactory organs downwind only, the rhino has developed an appropriate reaction to the alarm of other ungulates e.g. zebra, oryx, waterbuck, gazelle, and to the alarm chirping of the oxpecker. Alarm behaviour of the oxpecker, when man approaches, immediately causes alarm in the rhino.

After the first alarm, different reactions may be observed, depending on the past experience, the self-confidence, and aggressiveness of the animal.

All the reactions of rhino to man as an enemy can be counteracted easily. The eradication of the rhino in areas of spreading cultivation was easy; and there is no doubt that hunting and poaching will lead to the extermination of all five rhino species within a short time, unless they are protected effectively in suitable areas.

B. Symbiosis

1. Cattle egret, fork-tailed drongo, and oxpecker

The cattle egret *(Bubulcus ibis)* is often found in association with the elephant and other large ungulates like rhino, buffalo, wildebeeste. In walking, the mammal causes insects to move; these are then easily detected and caught by the egret. Though cattle egrets often sit on the back of the mammal, they are hardly ever seen to peck ectoparasites from its skin. When man approaches, the cattle egret may fly off and this reaction may alarm the mammal. But in no case observed was this effect very marked, perhaps because the cattle egret is not shy and does not show any pronounced excitement in alarm situations. It may be mentioned here that the association between cattle egret and rhino was frequently observed in Amboseli Game Reserve, but not in the Galana-Yatta Region of Tsavo East during the dry season, when the bird species is rare.

When feeding and moving slowly through bush vegetation, rhinos are often accompanied by the fork-tailed drongo *(Dicrurus adsimilis)*. This bird does not sit on the rhino itself but on twigs nearby. It flies around the rhino for short periods in a manner similar to a flycatcher, then perches again on a nearby twig. Probably the bird feeds on insects attracted by the rhino, possibly on biting flies. Normally the association does not last for long periods. Presumably the drongo is confined to a relatively small home range which it does not leave to accompany the rhino. Again the alarm signals of the drongo when man approaches are not conspicuous and correspondingly the rhino is hardly alarmed by this bird.

This is in striking contrast to the red-billed oxpecker *(Buphagus erythrorhynchus)* which has a high-pitched alarm chirrup. It is not confined to a restricted home range or territory but follows the rhino over a long period and distance, at least during the greater part of the year. Oxpeckers were observed to leave the rhinos towards evening and to congregate in small flocks which fly in the direction of roosting trees, where up to 20 individuals may gather. In the morning they disperse in small flocks over a large area in search of host mammals, amongst which rhinos play an important part. The oxpecker is often very active on the rhino. It climbs all over the rhino's body, legs and head, it enters the outer ears, even the nostrils, and is often very busy nibbling in the chronic ulcers of the rhino. It has been claimed that the oxpecker even causes these ulcers (SPINAGE 1960).

In the Galana-Yatta Region, when man approaches, the oxpeckers give the alarm chirrup when within 50 meters. In case of alarm of high intensity they fly off.

On the other hand, if man approaches in a slow inconspicuous manner, the birds calm down and often tolerate his presence within perhaps 30 meters.

In Amboseli Game Reserve the alarm distance of the oxpeckers is smaller than in Tsavo East; and in Nairobi National Park oxpeckers sitting on a giraffe, zebra, or impala even tolerate the presence of man in a car within 10 to 20 mtrs. It seems that the alarm behaviour of the oxpeckers is conditioned by the expectation of intense disturbance: the more vigorous the reaction of the host-mammal to man, the more pronounced the alarm behaviour of the oxpecker. When the rhino is alarmed it is no longer a suitable feeding niche for the birds. It often shakes its head and ears in order to get rid of them, apparently in an effort to check the situation more carefully. Undoubtedly the rhino itself has developed an alarm reaction to the alarm signal of the oxpecker. This reaction is at least intensified alertness, but can go as far as flight. When the alarmed rhino sees the disturber and is very self-confident, even attack at full speed can result.

2. Elephant

Normally elephant and rhino do not take notice of one another. There are however situations in which they are in each other's way. Then they often try to avoid one another as in the following examples:

Obs. Nr. 1: An elephant family-unit on the move came upon a rhino bull lying besides a termite hill. The bull rose and stood motionless. The elephant cows and the immatures passed him on both sides at a distance of appr. 6 to 8 meters. After they had gone, the rhino lay down again.

Obs. Nr. 2: An elephant family-unit moved slowly along a main track in the direction of the river, while behind them a rhino walked on the same track at a quicker pace. When the rhino had nearly caught up with the elephants, it used a smaller parallel trail and overtook them.

Sometimes in similar situations, subadult elephants try a playful bluff attack, to which the rhino may react by trotting away or with a symbolic counter-attack. But apparently encounters are not serious.

There are, however, situations in which serious competition and conflict may arise. Before the height of the drought in 1961, the elephants dug holes in the sandy bed of the Tiva River. Serious competition arose between elephants, rhinos, and buffalos over access to these holes, and also amongst the rhinos themselves. Similar conflict has also been observed at artificial saltlicks.

Rhinos normally give way to full grown elephant bulls; on the other hand, cows were often seen to withdraw when a rhino showed threatening behaviour.

Elephant and rhino are ecologically more interdependent than the rare occasions of direct contact would suggest. They use the same main and many of the moving-feeding tracks. If, as in the study area, there are many more elephants than rhinos (about 10 times as many), it is the elephants who really maintain the track system, and the rhinos make use of their efforts to open the country. Also in times of drought it is the elephants who dig the water holes, and the rhinos who make use of this last water supply.

In some few cases observed, the elephant even contributed to the food supply of the rhino: a small tree with branches inaccessible to the rhino, had been pressed down but not killed by elephants; later, new shoots were obviously browsed by rhinos. However, the impact of the elephant on its habitat is not purely favourable to the rhino. There is a considerable overlapping of food preferences of the two species (see Table I), as made evident by the collection of elephant food plants (Napier-Bax & Sheldrick 1963) and the collection of rhino food plants made in the Galana-Yatta

Region. In normal situations food competition between elephant and rhino should not be overrated, as elephants, when browsing, eat mainly the leaves or chew the bark of branches with a diameter of 3 to 5 cm. But they hardly ever tear off the thin twigs which are the main diet of the rhino.

It is mainly in times of general food scarcity that a large elephant population may aggravate the situation of the rhino by food competition. In these times the overlapping of food preferences may be more pronounced, both species concentrating on plants which are near water and still contain some nutritional substance.

It seems that the main danger for the rhino caused by elephant lies in the destruction of the tree and bush vegetation. Especially in concurrence with fire, the vegetation in large parts of Tsavo East has been converted from bush country to dry grassland under the pressure of a large elephant population (Buechner & Dawkins 1961, Glover & Sheldrick 1964).

C. Relationship with other herbivores

1. Other ungulates

Rhinos were seen several times in loose association with groups of zebras and with large herds of buffalos. In one case the zebras saw the observer from about 200 mtrs., watched him motionless and then suddenly started away. At this very moment the rhino too reacted with a sudden rush, followed a zebra in gallop as if chasing it, then changed direction, stopped, remained motionless with its tail lifted and tried to locate the origin of the disturbance. Similar scenes were observed between rhino and oryx. In all these cases, alarm in the other ungulate species caused the alarm reaction in the rhino.

Aggressive or defensive reactions of rhino towards other ungulates were also observed; three times rhinos were seen to rush at an antelope (twice waterbuck, once impala). In one case a mother rhino followed by a subadult male walked slowly over an open area. When a female waterbuck crossed their path laterally at about 20 mtrs. distance, the young bull suddenly turned and performed a short bluff attack. In another case a solitary male rhino walked along a main track to the watering place at the Galana River (Sobo bend). A group of waterbuck and male impala feeding on both sides of the track withdrew when the rhino approached. Only one male waterbuck remained near the track. The rhino bull rushed at the antelope and chased it for several seconds before continuing on his way to the river.

While the occasional association of the rhino with buffalo, oryx, or zebra may be of advantage to the rhino in the sense of protection against man, the observed aggressive reactions of the rhino to waterbuck or impala do not seem to have any ecological significance.

2. Ostrich

In the Yatta-Galana Region three short encounters between rhino and the Somali ostrich were observed, which took a rather surprising course. The rhino first listened in the direction of a walking ostrich group, then approached it at an easy trot. When within 6 to 8 mtrs. from the ostriches, it suddenly showed fear and ran off at full speed, while the ostriches took hardly any notice of the rhino. Presumably the rhino expected to meet another rhino and when it suddenly realised its mistake it reacted with fear and flight.

III. Malnutrition, diseases, and parasites

A. Sick and black-coloured rhinos

1. Examination of sick rhinos in 1961, 1964 and 1966

a. The drought period of 1960/61

During the severe drought period of 1960/61, the rhino population in Tsavo East suffered heavily from malnutrition, and subsequently about one third of the population died. During that period, many animals had been found in a very poor state or almost dying. They were all black-coloured from the saddle region down over the sides of the body.

A few of the dying animals were shot and examined, and it was agreed by those who carried out the postmortem examination that the animals had suffered from general malnutrition (GLOVER & SHELDRICK 1964). Their muscles were reduced, and they had large quantities of clear fluid in their body cavities. The black colour of the skin was found to consist of a film of dried blood. The intestinal tract contained a number of parasites (see III. B.). All these examinations and their evaluation are hampered by the fact that no comparative data of healthy rhinos are available.

b. 1964/66

From 1964 to 1966, during the dry season, we discovered three obviously sick and black rhinos, one in August 1964 (A), one in October 1964 (B) and one in October 1966 (C). Animal A was practically unable to walk and showed a striking lack of reactivity to the approach of the helicopter and to man on foot. It had marks of a recent attack by hyaenas (described earlier II. A.1.). Animal B rose when it perceived human scent and eventually trotted away very slowly when we approached it and shouted. Animal C, an old cow, was observed over several days. Each day it appeared weaker and was less and less able to move. Finally it was found lying near a main track. It did not react to engine noise or to shouting and only rose when it perceived our scent. But even then it was almost unable to walk.

Animals A and C were shot and a postmortem examination was carried out:

Animal A: Adult male. No signs of general malnutrition; muscles not conspicuously reduced in volume. Black coloured skin in saddle region and on the trunk due to a film of dried blood. Body cavities filled with large quantities of a clear fluid. Intestinal tract filled with food material. Intestines infested with parasites (see III. B.), fly larvae in stomach. The bacteriological examination of the liver (Vet. Res. Lab. Kabete) revealed an infection with a *leptospira* species.

Animal C: Old cow. Muscles especially of neck and thighs reduced. Teeth ground down almost to the gingiva. Black colour of the skin; fluid in body cavities; the intestinal tract infested with parasites as in A. Liver and kidneys appeared normal. Spleen was small and the red pulp reduced. Bone marrow contained many hematopoietic elements on smear. In blood smears 80% of the cells were granulocytes. The leucocyte number was not counted, but appeared increased on smears. In smears of a large skin ulcer, many granulocytes and staphylococci were found.

It might be assumed that in the old animal C, general malnutrition due to the reduced function of the teeth contributed to the poor state of health. In animal A the cause of disease is not clear; there were no definite signs of malnutrition, and the pathogenic function of the leptospira is not clear either.

2. Significance of black skin patches

a. Localization

In all cases, the shiny black patches were localized mainly in the saddle region and on the sides of the trunk. Patches were never seen on the rump, the legs, shoulders, thighs, neck, or head. In most rhinos in Tsavo East, the saddle region and sometimes the trunk are darker coloured than the rest of the body. It is obvious that dark areas are not well covered with dust by wallowing. This can be due to reduced wallowing by the individual, to a poor quality dust in the wallow used, or to removal of the dust film by external or behaviourial factors.

In fact, more dark-coloured rhinos were seen after a rain or on very windy days. Most of the really black rhinos were either sick or old, had very small babies, or were very heavy, probably highly pregnant cows. We might conclude that the black patches occur in rhinos who do not wallow for a long time either because they are incapable of wallowing due to sickness or old age or because they are instinctively inhibited to wallow as is shown later for mothers with small babies (Sociology and Behaviour VIII. A. 2.).

These assumptions are corroborated by the fact that where rhinos throughout the year have the opportunity to wallow in muddy water they have neither black patches nor dark coloured areas. Undoubtedly the muddy water in which rhinos of Amboseli Reserve and Manyara Park wallow has a better coating effect than the fine-grained dust of dry wallows in Tsavo East.

b. Origin of the blood film

The blood crust is formed on the skin when not protected over a long period by a sheet of soil. What actually causes the blood crust in unprotected areas?

Figure 8. Rhino covered with biting flies behind the shoulder region.

In fact, the saddle region and the sides of rhinos are most frequently covered with biting flies (Fig. 8). On the other hand, legs and neck are mobile parts of the body where flies can be chased off, the rump is protected by tail movements, and the head partly by ear flapping.

If the rhino's skin is covered with mud or dust, most flies were observed to sit on the rhino without actually sucking blood (SHELDRICK, personal comm.) and blood sucking occurs only on very small unprotected areas. Yet, in areas of the body, where the skin is unprotected over long periods, the incidence of blood sucking might be much higher. In both animals shot in 1964 and 1966, the black sides of the trunk were literally covered with biting flies, mainly *Lyperosia* and *Rhinomusca* (Fig. 9). This leads to the conclusion that the black patches are related to prolonged and uninhibited sucking activity of biting flies. It can well be assumed that a large number of flies, each one producing a small local bleeding, can over a long time produce a blood crust.

The problem of the black patches definitely requires further investigation. But at present, the above explanation seems to be most satisfying; and there is no evidence that black patches are due to a special type of nutritional deficiency manifesting itself by increased vascular permeability.

B. Parasites

Rhinos, like other wild animals, are infected with a number of ecto- and endoparasites.

1. Ectoparasites

Several tick species collected by D. SHELDRICK and identified by J. WALKER are listed in Table II.

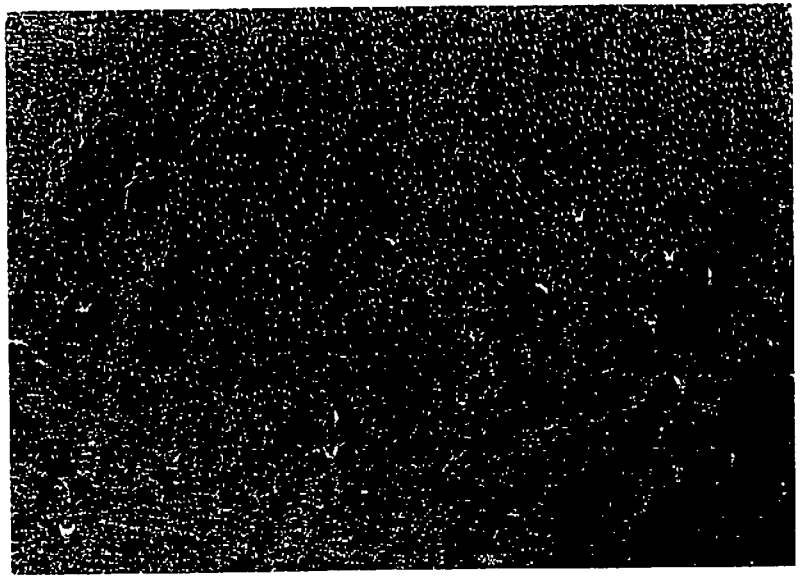

Figure 9. Large number of flies (*Lyperosia* and *Rhinomusca* species) on a dead rhino.

In the study area, ticks were not seen during the dry season. In the wet season, they attach mainly in the skin folds in the genital and anal region, in the ears and around the eyes.

Table II

Ticks identified by Jane Walker (previously EAVRO, Muguga, Kenya)

Rhipicephalus humeralis	(adults)
„ *simus*	(adults)
„ *pulchellus*	(1 female)
Amblyomma gemma	(adults)
„ *sparsum*	(adults)
Dermacentor rhinocerinus	(1 male)
Hyalomma rufipes	(1 male)

Several species of biting flies are usually found on rhinos. The most frequent ones have been identified by PARSONS & SHELDRICK (1964) as *Rhinomusca brucei*, *Lyperosia* species, *Tabanus* species and *Glossina pallipides Austen*. The first two species develop in rhino dung. When the imago is fully developed, it flies onto a rhino visiting the midden. These flies visit the host not only for a blood meal, but they actually live on the rhino by sitting mainly in the saddle region and on both sides of the trunk as described above (III. A.). After the postmortem examination of the cow C shot in October 1966 which was carried out about 2 kms from the camp, *Lyperosia* flies were suddenly abundant around the tents and we were bitten frequently what had never happened before. The only possible explanation is that some of the enormous number of *Lyperosia* flies which had been sitting on the dead rhino left the carcass and followed us on our way back to the camp.

In contrast, to *Rhinomusca* and *Lyperosia*, *Tabanus* and *Glossina* visit the rhino only for the blood meal and only at certain times of the day.

2. Endoparasites

Microfilaria: Many rhinos have ulcerating wounds especially in the flank region, behind the elbow, or on the side of the thorax. In these ulcers, a filaria, namely *Stephanofilaria dinniki* (ROUND 1964), has been found. The pathology of these lesions has been studied in South Africa (SCHULZ & KLUGE, 1960) and in Tsavo National Park East (TREMLETT, 1964), but the pathogenic significance of the infestation of the ulcers with the filaria is not clear. It might well be possible that the filaria infection is secondary to wounding by mechanical means and then causes the chronic ulceration.

Intestinal helminths: In the rhinos shot in 1964 and 1966 large numbers of platyhelminths and of nematods were found in the small and the large intestines. In 1966 samples were identified by J. BERGER (Wellcome Research Laboratory, Kabete) as *Anoplocephala* spec. (Platyhelminths), closely related to the common tapeworm of the horses. and *Kilulema* Genus (Trichoneminae) only found in the rhino.

Fly larvae: In the rhino shot in 1964, a confined area of the mucous membrane of the stomach was densely covered with a fly larva about the size of a date which was identified as *Gyrostigma* sp. (Fam. Oestridae).

Figure 10. Fly larvae (*Gyrostigma conjugens*) in the stomach of a dead rhino.

In the cow shot in 1966, a smaller type of fly larvae similar to the "horse bot" covered part of the stomach (Fig. 10). They were identified by J. Berger as *Gyrostigma conjugens*.

Thelaziid: In the bull shot in 1964, a roundworm was found in the conjunctiva of the eye. The species has been identified as a *Thelaziid* by the Vet. Officer at Vet. Res. Lab. Kabete.

IV. Intraspecific intolerance and aggression

Occasionally the assumption has been made (e.g. HEDIGER, 1949) that rhinos live in territories, show territorial intolerance and mark their territories with urine and dung. Other authors have suggested that rhinos "own" the main tracks in common, but nevertheless defend a restricted home range as a private property.

These assumptions certainly do not apply to the rhino population of the Galana-Yatta Region. All the tracks, wallows, and watering places are used by many different individuals, and in the various feeding areas, even in small patches between rocks or rocky hills, different rhinos were found at different times. There is no doubt that in the Galana-Yatta Region rhinos do not defend territories.

But rhinos are not gregarious animals either. The only social bond which is stable over 2 to 3 years, is the bond between mother and child. In one case a stable group consisted of an old cow, an aduld female, and a subadult bull, presumably mother, daughter, and son. Another group of the same composition in which the son was somewhat older than the daughter, was less stable. In Tsavo National Park East the association of an adult bull with a cow or with a mother with a calf always lasted for short periods of a few days or some hours only. The same was true for association of 4 to 5 individuals.

It could be asked whether the predominantly solitary way of life of the black rhinoceros is connected with intraspecific intolerance. All observations showed however that this is not the case. Intolerance between females or mothers is extremely rare. Usually cows do not show hostility to one another; in only a few cases was weak competition observed: e.g. when an individual was lying in a wallow and another arrived and also wanted to settle in the soft soil. Competition for special places of a much more serious nature arose, as mentioned above, during the drought of 1960/61, when the lower Tiva River dried out and water was available only in the holes which elephants had dug in the sandy river bed.

Intolerance between bulls is somewhat more frequent, but also not a predominant feature of rhino sociology. Three times we observed two bulls who formed a social group; they moved and fed together. The duration of this companionship is not known. Most of the bulls, however, do not associate with one another and either manage to avoid one another or show marked tension when they meet.

Various types of encounter were observed between bulls. Often two bulls faced one another motionless for several seconds, and then parted. In other cases showing off and threatening were observed. Once a bull chased his opponent for about 600 mtrs.; the latter then turned and ran back, and the pursuer gave up.

In July 1965 park employees reported the following incident:

Obs. Nr. 3: One bull chased another for more than 1 km. When he finally reached him, he prodded him repeatedly with his horns in the hind quarters. The pursued bull made quick turns sideways to avoid the attack and suddenly fell, whereupon the pursuer ceased to prod and slowly moved away, while the defeated bull rose and walked in the opposite direction.

Repeatedly bulls were seen with wounds or scars in the thighs, which may have been caused in the course of a similar chase.

Several authors (GUGGISBERG 1966, RITCHIE 1961) have reported that real fights between bull and cow are frequent. According to RITCHIE, the cow regularly attacks the bull during the premating phase. GUGGISBERG advances the opinion that the bull is equally aggressive during this phase, aud he agrees that sexual fights of great violence are quite normal. GODDARD (1966) has not observed real fighting between bull and cow in Ngorongoro Crater.

Twice, observers have reported to D. SHELDRICK that they had seen a bull attacking another rhino viciously and injuring it seriously. In one case, the victim was a cow, in the other it was the subadult son of a cow who was being courted by the attacking bull.

According to D. SHELDRICK (personal comm.), some years ago a bull and a cow had had an encounter on a rocky hill just above the Assistant Warden's house near Voi Entrance. Probably in the course of a chase, the cow fell down the precipice and was killed.

During our study we only once observed aggression between cow and bull that lasted longer than some seconds, and even in this case which will be described in the following observation, no animal was injured.

Obs. Nr. 4: One evening a bull waited on a main track to the water while a cow with a subadult son approached on the track. The bull listened, then walked towards them, but they immediately rushed at him. He turned and ran in a curve and was chased for some 300 meters in the direction from which mother and son had come. The two now continued their walk towards the river for some time. They were resting and feeding at low intensity when the bull who had followed their track approached them again, this time in a careful and timid way. He did indeed manage not to elicit the aggression of the cow and her son, though he remained in their vicinity.

Conflict between bull and cow was often seen in the context of premating but was never serious as will be shown in more details (Sociology and Behaviour VII.).

We may summarize that aggression occurs to a certain degree between bulls, and, less frequently, between the bull and the cow or her calf during premating contact. But there is no doubt that intraspecific intolerance is not a limiting factor for a rhino population.

V. The population of a selected area

A. Main problems

An ecological survey of a population is not satisfactory without a statement as to its size and composition. The total number of individuals should be known approximately, and also the sex ratio and the proportions of the most important age classes – immatures, adults in the phase of reproduction and infertile old individuals. The ecological evaluation of the actual status of a population requires the following data:

- age at sexual maturity in males and especially in females,
- interval between consecutive parturitions,
- length of the life phase of reproduction, especially in females.

As an animal population is a dynamic system reacting to changes in the environmental situation, a careful and continuous survey over several years would be most desirable to analyse the most important reactive mechanisms. With respect to the limited time available for this study, the survey had to be limited to a restricted area.

This again complicated the problem of developing a reliable counting method; movement in and out of the chosen area had to be considered.

For several reasons it appeared desirable to be able to recognize as many individual rhinos as possible and to build up photographic documentation. This was undertaken not only to solve the problems of movement and changes in the local distribution, but also to provide data concerning growth of immatures and reproductivity, especially in cows, by repeated surveys during the three years of the study. In order to corroborate the results of field observations, account must be taken of the experience of rhinos kept in captivity. Yet, although the black rhino has been bred in captivity, data concerning increase of weight and size in calves, age at sexual maturity for males and females and the interval between parturition and consecutive receptivity in females have not yet been published for this species. More is known in this respect of the Indian rhino (LANG 1961).

B. Methods

1. Counting- and observation areas

Area I (see Fig. 1) was selected for aerial counts. The Galana River forms its natural boundary to the south, a boundary which is sometimes, but certainly not often, crossed by rhinos – most probably only when the water level is low. To the north the area extends over the Yatta Plateau and its northern isolated islands. Preliminary flights revealed that during the dry season there were practically no rhinos further to the north. The western and eastern boundaries were chosen arbitrarily, that is, according to the capacity of the available aircraft and to use topographic features which could be recognised without mistake. The whole area has a size of approximately 200 km².

Area A (see Fig. 1 and Fig. 11) a smaller area within area I of about 25 km², was chosen for daily observation from the ground. A small Yatta island, isolated by erosion, was used as main observation station. In this place was located a telescope (maximum magnification 50 x in 1964 and 1965 and 60 x in 1966). Sometimes observations were also made on and from edges and spurs of the Yatta Plateau in the western, northern, and eastern part of area A. In addition rhinos were observed during periods of several hours or on successive days in other parts of area I.

Most observations from the ground had to be made on foot, since the terrain is cut by many small river beds which are very rocky and impassable even by Landrover.

2. Aerial survey

Aerial counts of the total population in area I were made by helicopter during three periods: 2 counts in July 1964, 2 in September 1964, and 7 in July 1965 on 4 successive days. The pilot flew at an altitude of 50 to 150 mtrs., in parallel legs with a distance of 800 to 1000 mtrs. between them. During the flights the rhinos were spotted by two observers (one on each side) and their location was marked on a map. Where possible, their sex was determined and the calves were grouped into three categories according to their size in comparison to their mother (Fig. 12):

- Babies: very small, from newborn to a few months old;
- Calves: from $^1/_4$ to $^2/_3$ the size of their mothers;
- Subadults: from $^3/_4$ to $^4/_5$ the size of their mothers.

On two occasions, one on 25/9/1964 and one on 17/7/1965, photographs of individual rhinos were taken during special helicopter flights while the pilot descended to 20–40 mtrs. above the animal. These photos were later compared with photos taken from the ground in the observation area.

In August 1965 a flight was undertaken in a plane with D. Sheldrick with – among others – the purpose of checking where newborn rhinos were located and how many there were.

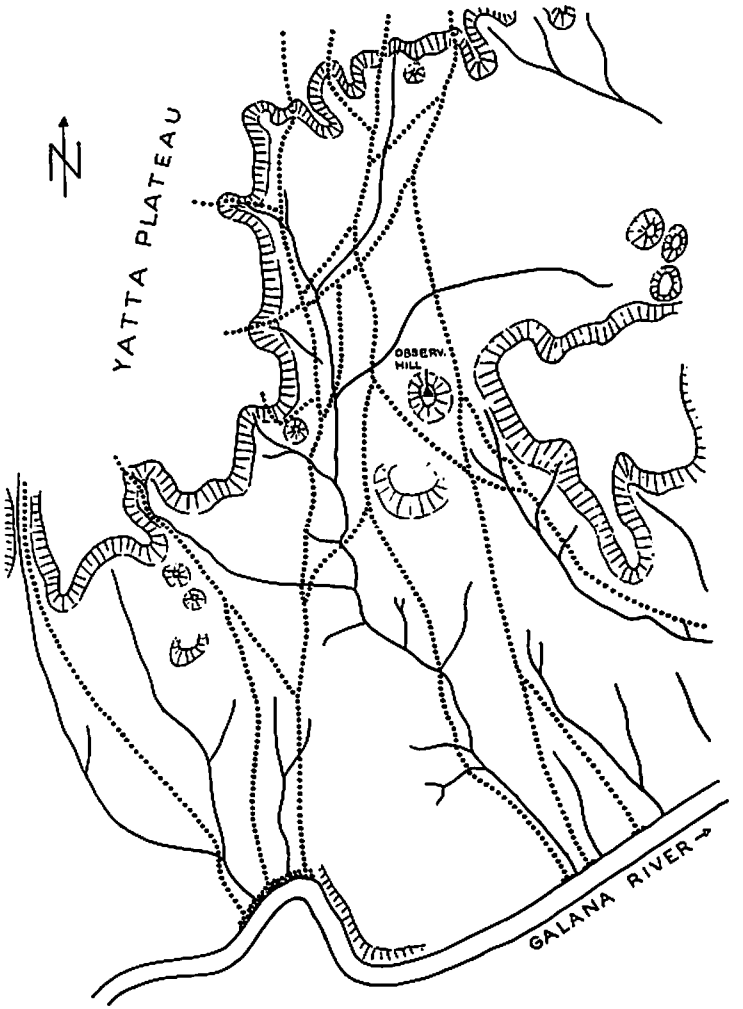

Figure 11. Observation area A within the larger area I. Main tracks leading to watering place.

3. Ground survey

Area A was surveyed almost daily during the following periods:

- 1964: 5 weeks in July/August, 3 days in October,

- 1965: 3 days in March, 5 weeks in July/August,
- 1966: 3 weeks in October.

This survey was not carried out as a programm on its own, but combined with the study of behaviour. It was attempted to note daily all individuals in or passing through the area, to note their sex, size, their association, position and movement

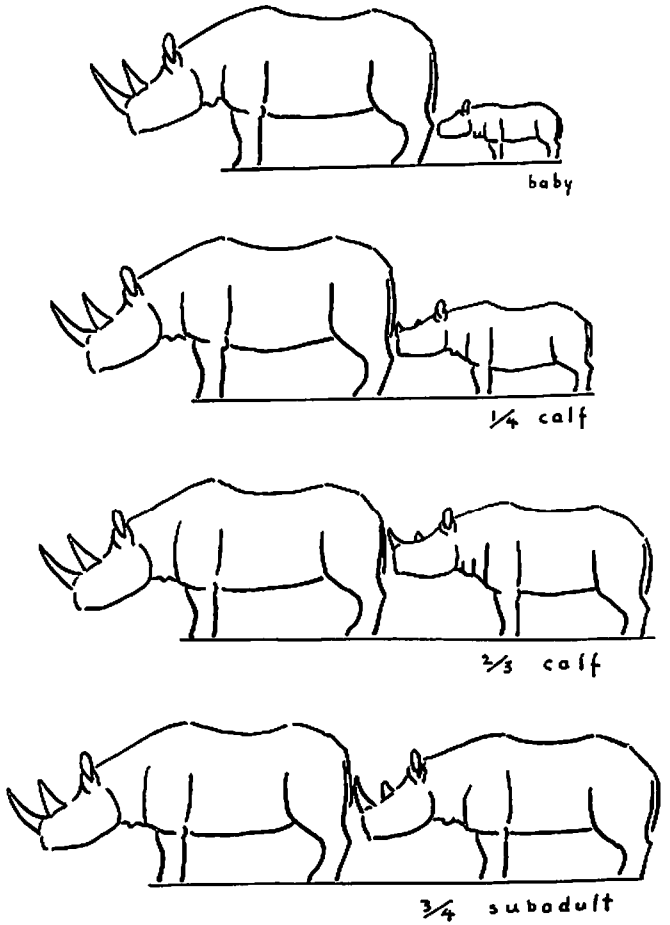

Figure 12. Categories of immature rhinos.

route in the area, and their main activities in the morning and evening (moving, feeding, resting, and social activities). Similar surveys were made occasionally in other parts of area I. Several times the activity program of a single rhino, a mother with a calf, or a bull associated with a cow, was recorded from early morning until evening. As it was impossible to follow rhinos continuously at night, attempts were made to find again in the early morning rhinos which had been observed during the previous day, in order to obtain information on their movement at night.

Frequency of watering of rhinos was investigated by two methods:

- On 20 consecutive evenings all the animals which passed near the observation hill in the direction of the river were noted. Their main characteristics were observed by telescope. Notes were taken of their association with other animals. Drawings were made and photographs taken in a few cases. It was checked that the animals really moved towards water. Attempts were made to identify the animals again on their consecutive trips to the water.
- In another suitable region a driving track of about 5 km along the Galana River was swept every evening with a thorn bush attached to the Landrover. In the morning the footprints crossing the track to and from the river were counted by 2–4 observers. These figures were compared with the approximate number of the total population behind this sector of the river, to obtain information on how often the average rhino goes to water.

Recognition of individual rhinos

Labelling of individual rhinos with a painting fluid under compression was attempted, but had to be abandoned after a few trials. The instrument at our disposal was too heavy to carry and handle, and effective only if used at a distance of less than 5 mtrs. from the animal. Darting was not tried because it would have introduced too many unpredictable disturbances and interfered with our observational program. In addition the value of labelling with paint was rather doubtful because of the wallowing habits of the rhino.

But, since rhinos have prominent individual features (horn shape, cuts in the ear, wounds and scars, folds of the skin) or are recognizable as members of a stable group (mother and calf), recognition from some distance by telescope and binoculars, and with the help of photographs taken at closer distances, proved fairly satisfactory for ground observation. In area A as many individual rhinos as possible were approached and photographed.

C. Results

1. Results of aerial counts

The counting results of seven flights made on 4 consecutive days in July 1965 are summarised in Table III.

The figures obtained on consecutive days and even of two counts made on the same day differ considerably. It has to be asked whether the number of rhinos present in the counting area did change to this extent, or, if the different figures are due mainly to mistakes made in counting. In the first case, it would be necessary to assume large scale movement in and out of the counting area. Yet most of the movement observed from the ground was to the river and back again. Only once during the time of observation was a rhino seen (by park assistants) to cross the river. In addition it is most improbable that rhinos crossed the northern limit of the counting area in large numbers. On every flight the density of rhinos near the northern limit was extremely low. As has been stated above, the eastern and western limits of area I were chosen arbitrarily, and there is no obstacle preventing rhinos from moving across these limits, that is generally speaking parallel to the river. Yet our observations did not produce evidence that movement did occur to the extent suggested by the counting figures. The counting results of flight No. 1 and No. 2 would e.g. indicate that movement out of the area exceeded movement into the area to such an

Table III

Aerial counts in July 1965

Flight Nr.	Date	Time	Adults single	Adults in pairs	Mothers with B	Mothers with C	Mothers with S	Total counted	Percentage: all adults (without mothers)	Percentage: all immatures	Percentage: babies
1	14/7	14.30	29	6	8	10	10	63	55.5%	22.2%	6.3%
2	15/7	10.30	19	—	4	8	2	33	57.5%	21.2%	6.1%
3	15/7	14.30	28	12	8	6	6	60	66.7%	16.6%	6.7%
4	16/7	8.30	28	2	10	12	6	58	51.7%	24.1%	8.6%
5	16/7	15.00	31	14	12	12	10	79	56.9%	21.5%	7.6%
6	17/7	8.30	24	2	4	8	6	44	59.1%	20.4%	4.5%
7	17/7	14.30	18	6	12	6	4	46	52.1%	23.9%	13.0%
Total			177	42	58	62	44	383	—	—	—
Average			—	—	—	—	—	—	57.1%	21.4%	7.6%

B = Babies – C = Calves – S = Subadults

extent that the number of residents was reduced by half. After this – between flight No. 2 and No. 3 – the inverse movement would have occurred within 4 hours – between 10.30 and 14.30. Our daily observations from the ground do not suggest that movement takes place at this time, as most individuals usually rest during the hot time of the day and only a few feed and/or move slowly.

On the other hand there is evidence that the reliability of aerial counts was much smaller than had been assumed. The large differences between the total number in flights No. 2 and No. 3 for example cannot be explained by movement into the area, but rather by a large counting error.

Simultaneous counting from the helicopter and from the ground in a definite area by different observers revealed that even trained observers in the aircraft missed under favourable conditions a considerable number, at least. $^1/_3$ of the rhinos.[1]

Evidently the following factors influence the reliability of counting from air:

- Light conditions: It is much easier to detect the rhinos in bright sunshine than in diffuse illumination.
- Disposition of the observer: It is quite obvious that besides the experience in spotting, the actual disposition of the observer is of major importance.
- Reaction of rhinos: The noise of the helicopter caused many rhinos to rise when lying and to trot away, to gallop or to rush forward in an effort to attack the cause of the disturbance. These animals could be detected fairly easily, at least if they moved within 200–300 mtrs. horizontally from the aircraft. If further away, they were easily missed. Not all individuals reacted in this way. A considerable number of them, after the first alarm, remained motionless, but ready for further reactions. Some remained lying on their resting place, others stood motionless after rising. Others again, stayed in bush vegetation or moved into it in search of cover. A mother with a small calf often stood on the spot after rising, covering the calf with her body, so that it was hardly exposed to the observer. All these individuals, which behaved in a more or less cryptic way, were easily missed. It is also possible that some of the rhinos became used to the disturbance after repeated

[1] Recently Goddard (1967, E.A. Wildlife J. 5:18–23) has checked the validity of censusing black rhino populations from the air using small aircrafts. He found that in Olduvai Gorge "even under the most ideal conditions" only 50% of the population were detected.

experience of the aircraft and did not react as vigorously as in the beginning. However, the closer the aircraft flew over the rhinos, the more seriously were they alarmed and the greater was the chance of detecting them. This would seem to recommend low flights for counting. But when flying low, it was obviously more difficult and often impossible to survey a strip of 400 to 500 mtrs. on each side of the helicopter. This difficulty could have been overcome by flying narrower legs, but then there was a risk that excited animals, in running away from the aircraft, were counted once or even twice more during the next legs. In addition such a flight pattern would have caused a substantial increase in fuel consumption and had other technical disadvantages.

It may be mentioned here that on the morning of the 15th July (Flight Nr. 2) when only 33 rhinos were counted in the area, the light conditions were very poor and the helicopter was flying rather high. On the other hand, on the afternoon of the 16th (Flight Nr. 5) when a maximum of 79 rhinos was seen, there was bright sunshine and the helicopter was flying rather low. The legs were nevertheless of the usual distance, so that considerable strips of terrain – approximately $^1/_3$ to locally $^1/_2$ of the area – could not be surveyed efficiently and therefore a corresponding number of animals was probably missed. It is obvious from all the possibilities of error, that the figures obtained in these aerial counts must be considerably lower than the real population. This makes it difficult to draw conclusions in matters in which the total population is involved i.e. distribution of the population, movement in and out of the observational area, and also the proportion of rhinos going to water every night. Nevertheless aerial counts have provided important information, especially in combination with ground surveys.

Although a varying proportion of the rhinos was undoubtedly missed in all the aerial counts, there is no reason to assume, that one special category of the population – bulls, or single cows, or mothers with subadults, calves, or babies – was more often overlooked than others. Therefore aerial counts should prove satisfactory as a method to investigate the proportional composition of the population.

In this context a few more remarks should be made: The association between two or three adult animals, especially between bull and cow, is generally unstable. Often a bull was observed from the ground with a cow for a short period of up to a few hours; then the animals moved in different directions. Therefore the proportion of single adults to adults in pairs is not a stable one in the aerial counts (Table III) and has a high variation. On the other hand, the proportion of mothers to all adults should not change in representative counts over a short period. The percentage of the mothers shows indeed relatively little variation, with an average of 21.4% and extreme values of 24 and 20.4% with the exception of flight Nr. 3.

The classification of immatures into three categories may have been subject to error; in particular the differentiation between calves and subadults is not always reliable during the flight. But the percentage of babies which are comparatively easy to classify, and especially the percentage of all immatures should be relatively stable over a short period. This is in fact the case: the percentage of immatures within flights differs from 16.6 to 24.1% with an average of 21.4%. Also the percentage of babies varies only in the range from 4.5 to 8.6% with the exception of the high value of flight Nr. 7.

2. Results of ground survey

It was never intended nor hoped to count the total population from the ground.

During the whole time of observation, area A did not appear to be the home range of a definite proportion of the population. It was passed daily by a varying number

of animals on their way to and from water. Other individuals stayed in the area throughout the day, feeding and resting. These left after one or perhaps a few days and sometimes appeared again in the area several days later. The way of life of the rhinos in the region is nomadic to a large degree, as will be outlined later, and the excursion range of each individual far exceeds area A. Nevertheless ground counts of the population within this limited area were made to investigate the composition of the population. The disadvantage of a relatively small counting area lies in the fact that it is more affected by an uneven distribution of the different components of the population.

A comparison of the two methods of survey, from the air and from the ground (Table IV) shows, however, that no basic difference was obtained in the distribution of the different age and sex categories by the two methods.

Table IV

Percentage distribution of age classes in aerial (A) and ground (G) counts in 1964, 1965 and 1966

Obs.	Total animals	Adults (mothers not included)	Mothers	Total adults	Babies	Calves + Subadults	Total immatures
1964 G	426	62.2%	18.9%	81.1%	1.4%	17.5%	18.9%
1964 A	455	62.6%	18.7%	81.3%	0.9%	17.8%	18.7%
1965 G	528	60.0%	20.0%	80.0%	4.6%	15.4%	20.0%
1965 A	383	57.2%	21.4%	78.6%	7.6%	13.8%	21.4%
1966 G	468	52.0%	24.0%	76.0%	5.6%	18.4%	24.0%

3. Size of the population

As pointed out above, aerial counts did not produce reliable results with regard to the size of the total population. A large proportion of the rhinos in area I must have been missed on each flight. On the other hand, area A where rhinos were carefully observed from the ground, was much smaller than the excursion range of any individual rhino. In fact we have not yet enough information as to the extent of nomadism of the local rhinos, and do not know to what extent the number of rhinos in area I actually changed as a consequence of movement. However, the following considerations should allow us to come nearer to the real size of the population present in area I.

Ground observations in area A made simultaneously with helicopter counts in the same area (as part of area I) showed that under favourable conditions $^1/_3$ to $^1/_2$ of the rhinos were missed by the observers in the aircraft.

On the average of 7 flights in 1965 four babies were counted and a total of 55 animals. Yet, on an additional flight with the park aircraft nine babies were seen in area I. All the ground observations also suggest that at least nine different mothers were accompanied by babies. If we assume that on the average of aerial counts the same percentage of babies was missed as of other age categories, then the whole population would amount to:

$$\frac{55 \times 9}{4} = 124 \text{ individuals}$$

In summing up, we come to the preliminary conclusion that, due to nomadism of the rhinos, the population within area I is not really stable. The total average number

within the area is about 120 individuals, which whould mean an approximate density of 1 rhino per 1.7 km².

In order to avoid misunderstandings it has to be pointed out, that rhinos were in no case evenly distributed throughout the area. Often two to eight "rhino-units", that is single adults or mother-child-units, were found within 1 km², while in other, much larger areas, no rhinos were seen at all. These relative concentrations of rhinos cannot be regarded as stable social groups. In many cases it was evident that animals were aware of the presence of their actual "neighbours", sometimes two units met deliberately; but very often they moved independently in different directions so that the momentary concentration disappeared again.

4. Composition of the population

As has been discussed above, aerial counts did not give reliable results as to the size of the population, but there is no obvious reason why the proportional composition should not be measured fairly accurately by these counts. On the other hand the counts made from the ground in the small area A are not necessarily representative for the whole area I, due to an uneven distribution of the different categories in this area. Since a large percentage of the animals counted in area A is moving to or from the river, that is to water, the length of the watering cycle of different groups might be of importance in this context (see C. 7.).

Table IV shows almost identical figures for aerial counts and observations made from the ground in 1964. In 1965, there is a larger difference between the percentage of babies observed from aircraft (7.6%) and from ground (4.6%). Observations made from aircraft and from ground show that mothers with newborn or very young babies move less than other rhinos and make use of a smaller excursion area. It is therefore possible – and aerial observation supports this assumption – that in 1965 babies were not equally distributed within area I and that area A was less frequently visited by mothers with babies. This explanation is supported by the following consideration: according to our observations at least 9 different mothers with babies were observed in area I. If these 9 babies represent 4.6% of the total population, the latter would amount to 200 individuals, which is definitely too high. This also suggests that the aerial counts are more representative for the composition of the population in 1965 than the ground counts.

In summary, all the figures indicate a significant increase of babies from 1964 (1.4% or 0.9%) to 1965 (4.6% or 7.6%) and during the same period an increase in immatures generally from 18.9 resp. 18.8% to 20.0 resp. 21.4%. The flight with D. Sheldrick in August 1965 over area I, the region south of Galana River and on its northern side, to the west of area I, showed that this high percentage of babies was not restricted to area I.

The concentration of parturitions in June and July 1965 suggests that in March and April 1964 a larger number of cows came on heat (Gestation period: approximately 15 months or 450 days, [Faust 1958, see also Schenkel & Lang 1969]). The reason for this "rutting" period is unknown.

It should also be added that in 1965 a larger number of apparently subadult animals was seen alone, namely 31 out of 526 = 5.9%, whilst in 1964 only 7 out of 420 animals = 1.7% belonged to this category. Probably these animals which appeared subadult in size and behaviour had been rejected by their mothers because of the new parturition, the exact time of this process not being known.

In 1966 no aerial counts were carried out and all the data were obtained from ground observation.

5. Sex ratio

There are three ways of recognizing the sex of rhinos: Firstly by the identification of external sexual organs, which is easier in males than in females. The second possibility is based on the experience that an adult rhino closely associated with a calf is its mother and therefore a female. The third one depends on the observation of special behaviour patterns such as squirting of urine in a horizontal shower, the complex bull ceremony (see Sociology and Behaviour V.D.), showing off and bluff attacks between two rhinos, patterns of behaviour which are characteristic of bulls, or releasing of urine in a typically female manner. External feature such as body size, shape and size of the horns or shape of the neck do not reliably indicate the sex of rhinos.

In aerial counts a large proportion of the animals could not be sexed, therefore sex is not included in Tables III and IV. Determination of sex is also difficult in single animals observed from great distance on the ground. It would have meant a useless effort to try to approach all the animals in different directions and at varying distances from the observation hill. In addition, when walking through the observation area, we would have disturbed the rhinos by our scent in the air and on our trail.

In 1966, with a better telescope at our disposition than in previous years, we made a special effort to sex as many rhinos as possible, including the immatures, within observation area A. Among the 356 adult rhinos observed from the ground 285 (= 76.1%) were sexed. As shown in Table V, the adult females outnumbered the

Table V

Distribution of the different age and sex classes of the rhinos observed in October 1966

Class	Females		Males		Not sexed		Total		Ratio
	Nr.	%	Nr.	%	Nr.	%	Nr.	%	♂:♀
Adults									
Mothers	112	23.9							
Single cows	49	10.5							
All	161	34.4	124	26.5	71	15.2	356	76.1	1:1.3
Immatures									
Babies	9		4						
Calves	17		27						
Subadults	1		15						
All	27	5.8	46	9.8	39	8.3	112	23.9	1:0.6
TOTAL	188	40.2	170	36.3	110	23.5	468	100	1:1.1

adult males in a ratio of 1.3 to 1. This sex ratio is most probably distorted. The main reason lies in the fact that a considerable part of the adult females, namely the mothers, can be sexed easily at all distances. In addition, mothers have on the average a somewhat shorter watering cycle than single adult rhinos. In area A, which during the dry season is an area of passage to and from water for most rhinos, mothers therefore appeared more frequently than single adults. Accordingly the percentage of mothers may be higher in the counts than in reality. This is in agreement with the few observations made in the area north of the Yatta Plateau, where we found more bulls than cows.

In conclusion we maintain that adult males are probably not outnumbered by adult females as shown in Table V., but that the real sex ratio for adult animals is close to 1 : 1. This is in agreement with findings of KLINGEL (1966) in Ngorongoro and with the recently published counts made in the Zambesi basin (ROTH 1968).

The distribution of females and males in the three age classes of immatures (Table V) seems rather haphazard. In immature rhinos sexing is based on the recognition of external sexual organs. This is more often possible in males than in females. We may therefore assume that among 39 unsexed immatures there are more females than males. It should, however, be mentioned that in some species of mammals, the percentage of immature males is higher than that of females. We obviously do not have enough data to make any comment in this respect, and particularly have no evidence for juvenile mortality.

6. Growth and reproduction

The ecological analysis of the structure of a population requires a knowledge of the following data:

- the age at sexual maturity, especially for the cow,
- the average interval between consecutive parturitions,
- the average duration of fertility during the life span of the cow.

Only limited observations of captive black rhinos are available. Our own observations in Tsavo East give no conclusive data as to age at sexual maturity, interval between parturitions and period of fertility, but they nevertheless throw some light on these questions.

a. Juvenile growth

In July 1965, a comparatively large number of babies was present in the area. They must have been born within a few weeks of one another, and accounted for more than a quarter of all immatures. In October 1966, we therefore expected either a large number of calves which were by then $1^1/_4$ to $1^1/_3$ years old, or, if there was high juvenile mortality, a considerable number of cows without offspring. In fact, in October 1966 the class of calves was larger than in previous years (61% of all immatures) and consisted mainly of half grown animals. This suggests strongly that the babies which were born in June and July 1965 were half grown in October 1966 at the age of $1^1/_4$ to $1^1/_3$ years. Additional evidence for this assumption was obtained from photographs. A mother which had been photographed with a newborn baby in July 1965 was found to be identical with a mother with half grown calf photographed in October 1966.

Premating and mating behaviour was observed in cows accompanied by approximately half grown to $^2/_3$ grown calves. This would mean that cows are usually receptive again between $1^1/_4$ and 2 years after parturition. With a gestation period of 450 days on the average (FAUST 1958, see also SCHENKEL & LANG 1969), the cow gives birth again when the former offspring is $2^1/_2$ to $3^1/_4$ years old. The fact that an association of a cow with both, a baby and a calf, has never been observed, indicates that the former offspring is no longer with its mother when the new baby is born, and even during the last phases of her pregnancy. Subadult rhinos thus live on their own when they are $2^1/_2$ to $3^1/_4$ years old.

Observations on the well known cows "Gertie" and "Gladys" in Amboseli support this conclusion (see GUGGISBERG 1966).

b. Maturity and reproduction in females

In July 1965, when a large number of babies were living in the area, we frequently saw subadult animals on their own. Most of these must have been offspring of cows

who had given birth again. In 1964, on two occasions a cow which was not full grown, was seen in association with a bull, and, in one case, it was clearly a sexually motivated contact. We may assume, therefore, that cows reach sexual maturity at $3^1/_2$ to 4 years and may give birth to their first offspring at $4^3/_4$ to $5^1/_4$ years. This assumption is supported by the following facts:

1. The female black rhino born in Frankfurt Zoo appeared almost full grown at $4^1/_2$ to 5 years (FAUST, personal comm.).
2. In the Basel Zoo the following data were noted for a cow of the Indian rhinoceros which had been born in captivity (LANG, 1961 and 1967):

Born	17. 8. 1958	
First heat	23. 7. 1961	(less than 3 years)
Mating	8. 11. 1961	($3^1/_4$ years)
Parturition	9. 3. 1963	($4^1/_2$ years)

In both species, the black and the Indian rhinoceros, females obviously continue to grow somewhat after they have reached sexual maturity. The heaviest cows which we observed in Tsavo East were either accompanied by a smaller adult or by a large subadult animal, or they were on their own. This suggests that old females live for several years after their fertile period is over, sometimes together with the last or the last two offspring, sometimes alone. But we have no definite information as to the age at which cows reach this stage. We can therefore only estimate the total reproductive capacity.

Making use of all available data, and assuming that a cow reaches the end of her reproductive phase at the age of 30 to 35 years, we obtain the following time-table for the female black rhino:

Independence at $2^1/_2$ to $3^1/_4$ years
Sexual maturity at $3^1/_2$ to 4 years
First parturition at $4^3/_4$ to $5^1/_4$ years
Interval between parturitions $2^1/_2$ to $3^1/_4$ years
The total number of offspring of a healthy cow will be at least 7 and at most 12.

c. Males

It has been observed in a number of larger mammal species that males reach sexual maturity and especially the full grown status later than females. In all these species, the male is stronger and larger than the female, equipped with special male weapons, and adorned with other external sexual features. This sexual dimorphism in external features, such as size and strength, together with the longer phase of development, indicates special functions of the male. In some species, leadership and group protection belong to the complex of male functions. Yet in the great majority of higher vertebrate species with a marked sexual dimorphism, the males are especially equipped for competition over privileges and striving for dominance. They thereby actually select from amongst themselves the individuals most fit for breeding. In many species the females contribute to this selection by being more stimulated to take up sexual and social contact with males in full status.

In the black rhinoceros sexual dimorphism is not pronounced. Leadership and group protection are not male functions. There is a certain degree of competition among bulls, especially competition over cows on heat. Most probably bluff attacks on cars, which are frequently observed in bulls associated with a cow, are directed against a presumptive rival bull!

Nevertheless, competition amongst rhino bulls is not as highly developed as it is for many other vertebrates.

Premating with its components of aggression between cow and bull seems to

function in testing perseverence and stamina as well as the premating experience of the bull. But again these special qualities of the bull are not really emphasized. Nevertheless, male rhinos reach sexual maturity and full status later than females. This was also obvious in the case of the tame bull "Rufus" in Tsavo East who still had subadult characteristics at the age of 6 years. But his development might have been retarded, because as a baby and small calf "Rufus" lacked mother's milk. In zoos too it has been observed that rhino babies remained runts for a long period if raised without mother's milk (HAGENBECK 1966).

In 1965 we observed a bull in premating contact with a cow of equal size. Also the bull which in 1966 had been observed when mating was comparatively small in size. Both ranged in size between the smallest males found on their own and really full-grown bulls. We might, therefore, conclude that a bull reaches sexual maturity at about 6 years of age and full status at about 8 to 10 years. A comparison with the Indian rhino may contribute towards substantiating this time-table:

Table VI

Comparison of development of the male in the Indian and the black rhinoceros

Age	Indian Rhino[1]	Black Rhino[2]
at independence	2 – $2^1/_2$ years	$2^1/_2$– $3^1/_4$ years
at sexual maturity	$5^1/_2$– 6 „	$5^1/_2$– 6 „
when fullgrown	10 –12 „	8 –10 „

[1] Dr. E. LANG, Basel Zoo, 1967, personal comm.
[2] according to our observation in Tsavo East

7. *Watering cycle*

During the dry season, the occurrence of surface water will contribute to the determination of the geographical limits for a rhino population. Even if food is available in areas far from water, rhinos might not be able to make use of it during the dry season.

Only very few rhinos were found in the regions between 12 and 15 kms away from the Galana River, both to the north and to the south, when we surveyed these areas by helicopter in July, August, and September. Further away practically no rhinos were seen at all.

The distance between areas with surface water and the most remote feeding areas depends mainly on capabilities of the rhino and on climatic conditions. When living in a feeding area far away from water, the rhino has to cover great distances to and from water, but, in addition, has to feed, rest, wallow and sleep etc. Such a program would be impossible to cope with if the rhino had to water every evening. It must, therefore, be able to remain without water for several days.

Rhinos have sweat glands (TREMLETT 1964) which contribute by evaporation to the regulation of body temperature and thereby lead to loss of body water. Local climatic conditions such as temperature, irradiation, wind and humidity must therefore play an important rôle in determining the length of the period away from water.

Though several authors have maintained that rhinos water daily, we were soon convinced that this was not the case in our observation area. Each evening only part of the local population moved to the river, and the individuals observed on consecutive evenings were not identical. Even rhinos which stayed near the river for several

days, most probably did not visit the watering place every evening. Individuals were seen feeding or sleeping in the evening a few kilometers away from water and were again found in the same area next morning. At the watering place itself, we observed bulls which came to the river banks early in the evening, wallowed and slept in the sand, later sniffed around and had encounters with other rhinos, and went off without drinking. Others passed the watering place on a feeding trip, but did not drink. In order to find out how often rhinos go to water, we tried to identify those which passed near the observation hill on their way to water, and we counted footprints on a track along the river (as mentioned in V. B.).

a. Observations of individual rhinos over a period of 20 consecutive days

During 20 consecutive days in October 1966 we registered all the rhinos which we could observe and especially those which we could recognize individually from the observation hill.

Of a total of 356 rhino-units observed, 21 were seen more than once and recognized with certainty. A similar number of others was probably seen more than once, but identification was not quite definite.

The 21 rhino-units consisted of 12 mothers with offsprings (= 9% of all mothers), of 6 bulls (= 5% of all bulls), and of 3 single cows (= 6% of all single cows). On the average, a unit was seen 5 times (range from 2 to 11 times).

The observations made for five different rhino-units (here called A, B, C, D, and E) are represented in diagrams in Fig. 13. These diagrams show the approximate distance from water for each individual observation and the direction of general movement of the rhino. It is comparatively easy to recognize periodic movements to and from water in the cases A and B, both mothers with babies. The watering cycle appears quite clearly in the diagrams. Both units obviously visited feeding areas at a considerable distance from water and in between times could be seen on the move to and from water in the evenings and mornings. The interval between consecutive trips to the water was in most instances 4 days, once 3 days and once 5 days.

In the two cases C and D, the animals stayed rather near the water, in the neighbourhood of the observation hill, for several mornings and evenings. Apparently they had no need to move to the river during the day and so we could not see them on the move to and from water. We might assume that C watered during the evenings of 29/9, 4/10, 9/10 and 14/10, that is, with a watering cycle of 5 days, but it is impossible to know whether they also watered e.g. between 9/10 and 14/10, when the mother and calf were seen almost daily near the observation hill.

For D, the data were even more difficult to interpret. The animals might have watered during the nights of 28 or 29/9, 2/10, 6/10, 10/10 and 14/10, that is with a cycle of 4 days, but other interpretations cannot be excluded.

The case of the old cow E, which was shot on 13/10, is of special interest. We have therefore illustrated the movements of this animal between 1/10 and 13/10 in the diagram (see Fig. 13) and in a schematic map of the region (Fig. 14). This cow undoubtedly changed her watering place during the time of observation.

These observations were hampered by several difficulties, among which the most important are:

- Recognition on the basis of typical features such as horn shape, wounds, scars, skin folds is often impossible at a distance. The association of mother and offspring was used as a helpful characteristic. This contributed to the higher number of mother-child-units among the individually known animals, but did not help to analyse the watering cycle of single rhinos.

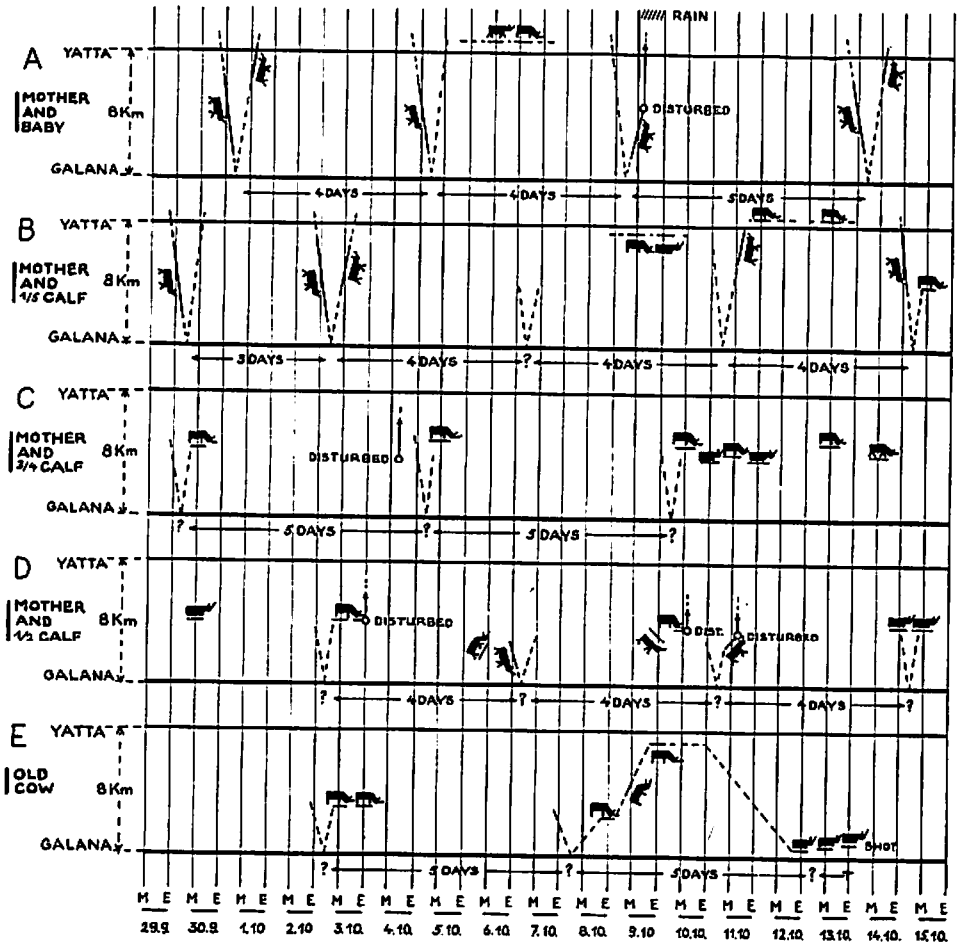

Figure 13. Diagrams showing localisation and movement of five different rhino units on 20 consecutive days (M = morning, E = evening).

- Rhinos may visit different watering places. This is one aspect of their nomadism. Only mothers with babies do not frequently change their route, feeding areas, and watering place. This will contribute towards acquainting the baby progressively with parts of the home range.
- As made evident by the observations of C and D (see Fig. 13), individuals sometimes did not walk through the observation area on their way to water but stayed for some days in the neighbourhood of the river. These animals might make the short trip to water unobserved during the night, and therefore their watering cycle could not be defined.

Despite these shortcomings, our observations suggest:

- that mothers with babies and small calves have an average watering cycle of 4 days,

– that mothers with larger offsprings and single adults go to water at intervals of 4 to 5 and perhaps even 6 days. Their nomadism is pronounced and they may change their watering place frequently.

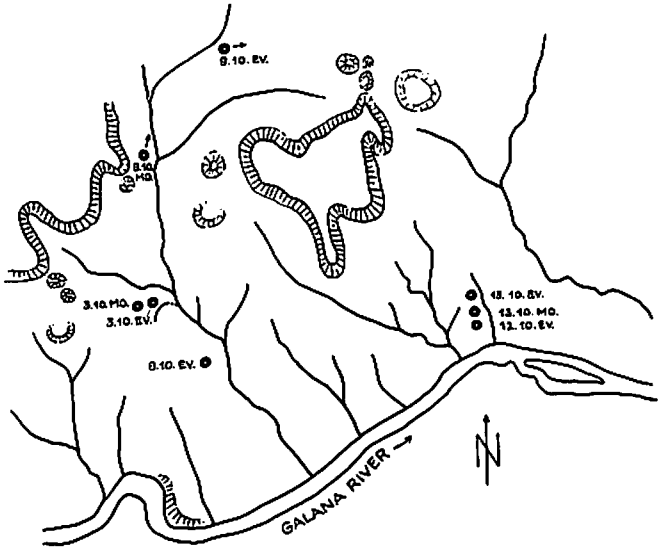

Figure 14. Map of observation area A showing the movement of an old cow (E) on 10 consecutive days.

b. Counts of footprints on a track along the river

Counts of footprints made on 23 consecutive days on a track along the southern bank of Galana River are summarised in Table VII. On the average, footprints of 14 animals going to water and 12 animals coming from the water were counted. In addition a few trails (average 2.6) were observed more or less parallel to the track.

The difference in the number of animals going to and coming from the water is most probably due to counting error. There was no evidence that animals crossed the river at night. It was not always possible to differentiate between footprints definitely leading to or from water, and those produced on a feeding trip e. g. along the *Suaeda* bush girdle bordering the river.

Table VII

Counts of footprints of rhinos crossing a track parallel to the river, south of Galana River, on 23 consecutive days in July 1965

	Footprints		
	to the river	from the river	along the track
Average	13.9	12	2.6
Standard deviation	4.4	2.7	0.6

The number of animals in the area behind this sector of the river was counted in 4 flights. Again, as outlined earlier (V.C.1) there was large variation in the number of animals spotted each time from the aircraft. The highest number of 32 is probably still an underestimate by $^1/_3$ to $^1/_2$. Assuming that the total number would be approximately 50 animals and that the number of rhinos who actually came to water was at an average of somewhat below 12, we calculate an interval between watering similar to the one under a., namely an average of 4–5 days.

D. An ecological evaluation of the rhino in the Galana-Yatta Region

1. The status of the population in 1966

Within the rhino population of the Galana-Yatta Region almost $^2/_3$ of the adult females are mothers leading offspring less than 3 years old. The remaining one third of the adult cows must consist of the following categories:

a. Young cows ranging from those which are newly independent to those near their first parturition, that is the age class of females from $2^1/_2$ or 3 to $5^1/_2$ or 6 years old.
b. Old cows which are no longer reproductive.
c. Highly pregnant mothers who have recently repulsed their offspring and will shortly give birth.
d. Cows which are infertile.
e. Mothers who have lost their offspring by predation, accident, or other reasons related to juvenile mortality[2].

It is ecologically important to determine the ratio of the number of cows in the first three categories to the numbers in categories d. and e.

Let us assume that, on the average, cows live on their own for 3 years before the first parturition, that they give birth at intervals of $3^1/_2$ years, live alone for $^1/_4$ year before each parturition, give birth to a total of 8 babies, and live on their own for the last 4 to 5 years of their life: in this case we calculate the ratio of mothers to the total female population as 27 in 37, that is nearly 2 in 3, the proportion found in the counts. Though these assumptions are not entirely based on established facts, they indicate that the rhino population in the Galana-Yatta Region suffers neither from a high juvenile mortality nor from a high degree of infertility of cows. The population appears to regenerate adequately.

2. Ecological trends of the situation

As has been stated, the exceptional drought of 1960/61 reduced the rhino population of Tsavo National Park East by at least one third. During these two years there was no vegetational growth. Subsequently food became scarce. The rhinos, the elephants, and other large herbivores concentrated more and more near the few permanent water courses. Food resources were exploited heavily in these areas. The result was severe food shortage and damage to the vegetation.

In 1962 rains were excessive and floods occurred all over East Africa. In the following years the climate was again more balanced and the vegetation regenerated each year during the rainy seasons.

Though no botanical survey of the recovery of the vegetation since 1961 has been

[2] In Tsavo National Park East twice (in 1960 and 1966) a newborn rhino was found on its own. Most probably in these cases the reciprocal bond between mother and newborn calf had not developed successfully during the phase of imprinting.

carried out, it has to be assumed that short lived plants such as grasses and herbs build up more quickly than long lived plants such as bush and shrub vegetation. The latter are the main source of food for rhinos. It seems that this building up process was still going on during the years 1964 to 1966 when this study was carried out. The recovery of bush and shrub vegetation must have contributed to the recovery of the local rhino population, leading to a new equilibrium at a higher level, between rhinos and vegetation. The great number of parturitions in June, July, and August 1965 and the high reproduction rate generally can be understood in this context.

During the same time another process has become increasingly evident in the study area, a process which might eventually lead to serious consequences for the rhino: the invasion of the region by elephants causing progressive destruction of important components of the vegetation.

In 1966 the impact of the elephant on the vegetation showed the following main aspects:

- Along the Galana River practically all trees with the exception of the Doum Palms (*Hyphaene* spp.) have been killed by ring-barking. The *Suaeda* girdle on the river banks appeared heavily reduced in size and damaged near the watering places.
- In the region between the Galana River and the Yatta Plateau, with its soft slopes, small valleys, and flat hills, most of the *Commiphora* trees have been uprooted during the last years. Several stretches of terrain where rather low growing trees of this genus were abundant in July 1964, were literally covered with bleached and dried tree carcasses in October 1966. Many trees of other families – e.g. of the acacias – have been heavily damaged throughout the region, some by ring-barking, others by breaking most of the branches.
- In 1966 the main tracks appeared widened and the network of moving-feeding tracks more or less parallel to the main tracks extended over larger areas and appeared denser and more trampled than in the two previous years.
  In these zones along the main tracks grass and herbs have disappared leaving the soil almost bare. The bush vegetation has also suffered. Uprooted bush and especially bushes with broken off parts were frequently seen. But in general the impact on the bush vegetation was not as heavy as on the trees.
- On the Yatta Plateau the increasing destruction of trees was striking. Elephants must have invaded the observation hill some time between August 1965 and September 1966, destroyed all the *Sanseveria*, trampled the bush vegetation, broken down or uprooted most of the small and damaged the few larger trees.
  Similar damage of the vegetation is frequently seen now on the rocky parts of the Yatta Plateau. In depressions of the Plateau, especially where main tracks lead across it, the devastation of the vegetational cover is most pronounced. Dead trees and large patches of bare soil are predominant during the dry season. Again, it seems that the shrub and bush component has suffered less than trees and even grass.
- To the north of the Plateau the progressive destruction of the vegetation is also fully evident. Again, destruction of trees, the *Sanseveria* thicket, and the grass cover by trampling are most pronounced.

Undoubtedly the impact of the elephant has resulted in a conversion of the vegetation in large parts of Tsavo National Park East (Glover & Sheldrick 1964). The vegetational cover with its *Commiphora*, bush and *Sanseveria* thickets has been converted into a rather thin grass cover. In the eastern section of the Yatta Plateau and the adjacent areas this conversion is not yet complete, but it is in progress due to the increasing invasion by elephants.

This situation has to be considered in the context of an ecological evaluation of the rhino in this region. So far the local rhino population has not suffered. On the contrary, it has recovered with the vegetation from the consequences of the heavy drought of 1960/61. But we must conclude that the development caused by elephants can be a serious menace to the future of the rhinoceros in the region. It seems that up to now the bush and shrub vegetation has not suffered much from the elephant. But this might well be a preliminary phase of the changes in progress; in other regions of Tsavo National Park East the changes caused by elephant and fire concurrently have led finally to the loss of all bush and tree vegetation.

It is difficult to believe that the black rhinoceros can survive in dry grassland. Yet, it must be admitted that in the Serengeti and in Ngorongoro Crater rhinos are often seen in the open, sometimes even feeding on very low growing herbs; but on the whole they live in the adjacent bush country.

3. Conservation of the rhino in Tsavo National Park East

Tsavo National Park East with its rhino population of approximately 1000 individuals is one of the last strongholds of the species. It is therefore of the utmost importance for the conservation of the species to protect the population of Tsavo East.

It is difficult to foresee how the ecological situation outlined above will develop. Prophylactic measures should be taken soon before this development has taken irreversible course.

1. A comprehensive ecological investigation of the whole region should be made over a number of years. This investigation should include an ecological analysis of the elephant population, of the changes in the vegetation and of the rhino population.
2. A suitable area should be chosen without delay for active management. This area should contain a healthy rhino population. Its vegetation should still show the main components which have been characteristic of the region during the last decades. In this area the number of elephants should be reduced and then kept at a low level by active control. It is self evident that elephant control would have to be carried out so as to keep disturbance within the area at a minimum. It is not the purpose of this work to define the size to which the elephant population should be reduced, or how to carry out elephant control. We would, however, like to define clearly the purpose of such measures:
   Within the chosen area, management has to aim at the preservation of a tree and bush habitat as was characteristic of the area during recent decades. By these measures a healthy self-regenerating rhino population should be preserved. Management should be continued at least until the consequences of the present development in other parts of the Park have been clearly established.

SOCIOLOGY AND BEHAVIOUR

I. The program of daily activity[3]

A. Questions and methods of investigation

Some authors have claimed that rhinos belong to those mammals which have an extremely stereotyped daily program. It has even been suggested that the individual rhino visits the same localities every day at the same time and thus performs the activities of daily routine in a stable sequence.

In the light of our experience already mentioned in this paper, we cannot agree with this opinion. The rhinos of the population studied in Tsavo National Park East are "nomads" and visit water only at intervals of several days, The program of consecutive days cannot be identical from the point of view either of the sequence of activities, or of the localities visited. This leads to the question whether the life of the rhinos in this area is governed by a cycle of several days. Is perhaps the watering cycle a stable program unit, at least during the dry season?

Activity programs are connected with drives or needs and the stimulating situations which together govern behaviour. A stereotyped program therefore presupposes the regular arousal and quiescence of drives in correlation with an external situation which, by necessity, has to be a stable system in its stimulus value.

Obviously all kinds of adaptive reactions to changes in the environmental situation disturb regular and stereotyped program patterns. It has to be analysed therefore to which environmental changes rhinos react, how they react und how often such reactions occur.

In this context the following efforts were made:

1. Eight different rhino-units were observed continuously from morning to evening and their activities were registered.
2. On 47 days all the rhinos present in the study area were surveyed from morning to evening or at least during the time of major activity – i.e. in the morning until about 11 a.m. and in the evening from 3 p.m. on – and their activity was registered.
3. On 23 consecutive days in July/August 1964 and 17 in 1966, special attention was given to recognizing individual rhino-units, to noting the time of their appearance, their activity and the areas in which they stood; 47 different rhino-units (altogether 74 animals) were recognized and seen at intervals, 26 in 1964 and 21 in 1966.
4. Occasional visits were made to other parts of area I; rhinos were identified if possible by photographs, and their activities registered.
5. We passed about 20 nights in the open, two of these very close to a main track; we visited the main watering place several times at the beginning of the night and drove many times along the Park roads at night. On all these occasions observations of nightly activity of rhinos were registered.

[3] The term »activity program« is used here to denote the total of activity patterns, and not to state implicitly that daily activity is determined beforehand, i. e. programmed.

B. Results

As we have stated above, the rhinos of this region visit the water almost exclusively between late evening and dawn and at intervals of several days. Therefore, certain days are characterized by movement towards, others by movement away from water. Besides these two types of activity programs, we have also observed others without the component of moving. The following examples illustrate these three categories of programs:

1. Program with movement away from water

Bull, observed 21/7/1965, 2 kms NW from Sobo-bend.

6.30– 8.10	Feeding and slowly moving in N-direction.
8.10– 8.30	Follows game-track in N-direction (Yatta-Plateau), without feeding.
8.30–10.05	Leaves track and feeds persistently without moving in a definite direction.
10.05–10.15	Goes to tree and remains standing in the shadow.
10.15–10.30	Leaves the tree and defecates at some distance, then walks back to the tree and remains there standing in the shadow.
10.30–15.55	Lies down and remains lying until 15.55.
15.55–16.00	Rises, remains standing, takes some steps almost on the spot, then lies down again.
16.00–17.50	Lies under the tree.
17.50–18.30	Rises, begins to feed and continues until dark.

Ad 1.

All rhinos we had observed had left the water before dawn. But apparently the moment of the start, speed, resoluteness and duration of moving, and correspondingly the distance covered, were very different from one case to another. Obviously it was important which area the animals intended to reach. Those who made use of feeding areas near the river had no reason to hurry away from the water. Some followed feeding tracks along the bush girdle on the river banks, where they fed, defecated and rested. Animals who apparently aimed at more remote areas, showed very different tactics in moving: some had already started early in the night, others only one or two hours before dawn; some covered up to 6 kms and perhaps more in one steady march before they slowed down and began to feed and rest; others moved and fed simultaneously or alternately near the river and had their long rest only 2–3 kms away from the river, and only towards evening movement further away from the river was taken up again.

The proportion of active trends and their compromise as revealed in the actual program is far from uniform.

2. Program without moving

Bull, observed 10. 7. 1964, 1km N of Sobo-bend.

8.15	Feeds in one place without moving.
8.40	Feeds on grass.
9.10	Feeds on bush.
9.25	Dozes with head down.
9.30	Head up, changes position for 180°.
9.34	Lies down.
9.50	Gets up, turns through 90°, lies down again.
11.35	Gets up, feeds a little.

11.55 Standing under a small tree, head hanging down.
11.58 Head up, ears raised – then lies down in the shadow.
12.30 Gets up, stands for some time, head goes slowly down.
12.42 Again short activation – then lies down.
14.27 Rises, leaves the shadow, feeds.
15.00 Walks into the shadow of the tree.
15.35 Lies down on the same place as before.
16.45 Rises and feeds.
about
18.00 Still feeding in the same area.

Ad 2.

Programs without movement to and from water are not less varied, although the variations are perhaps less conspicuous. In a majority of cases the time of the greatest heat – from 11 to 3 – is spent sleeping, and feeding again predominates towards evening. But in a considerable number of cases, the animals showed no increased activity towards evening and just continued to sleep and rest; or in others they were active during a short period and then again settled down to sleep. In bulls a more or less circular tour with sniffing and sometimes squirting urine was frequently observed in the early evening.

3. Program with moving towards water

Mother and 2/3 grown calf, observed 21/7/1965,
Yatta Plateau eastern part, approx. $5^1/_2$ km N of Galana.

7.30– 9.00 Feeding without moving.
9.00–11.15 Feeding and moving slowly in S direction. During this time the mother urinates twice small quantities. Mother and calf defecate once.
11.55 They go near a tree, remain standing in the shadow.
11.30 They lie down.
13.00–13.15 They rise and remain standing, then lie down again.
14.30 They rise and remain standing for some minutes.
14.40–16.00 Feeding and moving slowly in S direction.
16.30 Walking on game track in direction towards the river.
17.15 Observer leaves the group.

Ad 3.

Again there is considerable variation in programs with movement towards water. Generally it can be stated, that in the morning and in the early afternoon, when only few rhinos move at all, all movement towards water is slow and in most cases combined with feeding. In area A rhinos were observed to move steadily on a main track in direction of the water only after 3 o'clock. But these trips again showed many variations: some animals walked steadily to the watering place, others suddenly left a main track, visited a wallow nearby, wallowed and then remained lying there for from some minutes up to hours. Others again left the main track 1 to 3 kms from the river, to feed intensely, and were still feeding at dusk.

Finally it may be repeated here that the behaviour at the watering place and the time spent there vary greatly from one animal to the other.

We have differentiated between three categories of daily programs: those with movement away from water, those without and those with movement towards water. But as we have stated (Ecology V. C. 7.) the watering cycle may well last up to 6 days in some animals and accordingly it consists of more than one day of each category. We have so far not been able to follow one rhino over a whole cycle, but on the basis of a large number of single observations we are nevertheless inclined to think that

the whole watering cycle does not consist of any daily programs other than the ones outlined above.

In fact a large number of observations suggest that moving away from the river can be extended over more than one day; and the same applies to the move towards water. In addition we have observed a considerable number of animals which stayed in the same area over two consecutive days, almost certainly without watering in between.

All our observations of rhinos in the Galana-Yatta Region lead to the conclusion that activity during the watering cycle of the individual rhino is generally governed by the following tendencies and drives:

- the tendency to reach the river to quench thirst;
- the tendency to reach a special temporary feeding area;
- the tendency to follow special routes in both directions;
- superposed needs of short duration: – to feed, – to wallow, – to rest and to sleep, – to investigate the special aspects of the environment and – to mark with ritualized defecation and (mainly in bulls) urination.

It is impossible to analyse in each individual case which factors cause the preference for special feeding areas or for a special route. The following considerations may be useful to see the complexity of the problem:

- The individual rhino is introduced into the home range, its feeding areas, its track system, its watering places and wallows etc. by its mother, and thereby may acquire certain habitual preferences with respect to feeding areas, routes and programs. In several cases single rhinos and mother-calf-units were repeatedly observed on the same tracks and in the same feeding and resting areas on their way to and from water.
- The olfactory impregnation of the living space of the local population may stimulate social tendencies and exert a guiding effect on the individual.
- The actual local conditions of the habitat, especially with regard to occurrence and quality of food, may have similar effects.

This leads to the general question as to the reactions of the rhino to changes in environment. Most striking are the reactions to human scent. The disturbance may result in a complete confusion of the daily program. Intraspecific interactions also affect the program more or less. In this respect hostile encounters between bulls, and premating contact merit special mention. Interference by elephants may result in a modification of the program. In a few cases it was evident that local climatic changes affected the activity of the rhinos; e.g. on a day during the height of the dry season when some minor rain showers fell over the Yatta Plateau, the number of rhinos walking rapidly to water was reduced.

4. Activity at night

Also at night rhinos were observed feeding, moving, and resting. The activity pro gram of different individuals is as different as it is during the day. During the two nights passed near a main track approximately 5 kilometers from the watering place rhinos passed in the direction of water from dusk until 2 in the morning, and others passed in the opposite direction from midnight until 8 in the morning. Shortly after midnight a rhino climbed the slope approaching the observers, while feeding intensely. Its movement was directed away from the river.

The comportment of individual rhinos at night near the watering place also shows many variations.

Summary

The most conspicuous features of rhino activity in the observation area in the course of the day can be summarized as follows: rhino activity is most reduced during the hours of intense heat, i.e. between 10 in the morning and 3 in the afternoon. Feeding is most frequently observed in the morning before 10 and in the late afternoon. From 3 in the afternoon until dusk, movement of rhinos along main tracks towards water is most conspicuous. But this is, in reality, a superficial aspect of the daily activity rhythm in a rhino population. While a certain part of the population is active, resting and sleeping animals are easily overlooked. Careful observation reveals that the activity programs of consecutive days differ greatly in connection with the watering cycle. In addition, individual and traditional habits and the influence of external factors cause further variations.

II. Group formation

A. The mother-child-unit

The only stable social group in the black rhinoceros is the mother-child-unit. It persists when the mother mates again and even during most of the period of the new pregnancy. Most probably the group is dissolved not long before the next parturition.

On several occasions observed, a mother which had no further calf lived permanently with an adult, but definitely younger animal, or even with two of different ages. They must have been her offspring of former years, because the group still had some characteristics of a mother-child-unit. Mother and child form an activity unit. The transfer of mood and impulse is most pronounced in moments of disturbance, but is never absent in all activities throughout the day.

B. The association of bull and cow

Associations of bull and cow – or mother with calf – are not stable as also described by GODDARD (1966). A bull may "visit" a cow and stay with her from less than an hour to perhaps a day, when she is not on heat, or for a few days in the case of premating and mating. Longer lasting association does occur occasionally, perhaps on the basis of kinship.

Normally it is the bull who brings about the association by carefully approaching and following the cow, thus avoiding eliciting her repulse. Transfer of mood may develop to a certain degree.

In the case of disturbance by man, the bull occasionally defends the cow with a bluff attack and only then flees with her, but more often the community of action then breaks as is illustrated by the following examples.

Obs. Nr. 5: After mating, a bull and a cow with calf were feeding near one another. The cow came across our scent track, showed alarm excitement and rushed in the direction of the bull, the calf joining her immediately. The bull, startled by her excitement, approached her. After a short moment of facing one another at very close range, the cow took to flight with the calf, while the bull, after a moment of hesitation, quietened down and continued to feed.

Obs. Nr. 6: A bull and a cow were lying close together. When human scent reached them, they rose and ran off at full speed in nearly opposite directions. From our point of observation we could follow the route of each animal by eye over approx. 1 km. They did not try to rejoin one another.

Sometimes the mating bond breaks through interference by other rhinos, as in the following example:

Obs. Nr. 7: On 2/10/66 a mating couple – the cow accompanied by her calf – had reached the end phase of copulation, when another mother with a calf approached in apparent curiosity. The bull immediately dismounted the cow and ran off for about 30 meters. Both mothers and calves remained together and the bull approached again. Then each mother with her calf moved slowly in a different direction while feeding. The bull also started to feed, first following one cow, then the other and finally moving independantly in a direction of his own.

C. Other temporary associations

Associations between two mother-child-units have been observed in several cases, but they appeared fortuituous and never lasted for more than a few hours. In Amboseli Game Reserve where nomadism is less pronounced and excursion ranges do not overlap as much, association of the same individuals was observed repeatedly. One of these temporary associations consisted of a heavy bull, two adult cows, which were always found together, most probably mother and adult daughter, and a third, hardly full grown cow. These four animals were acquainted with each other and, during the time of association, moved, fed, and slept together as an activity unit.

In Ngorongoro Crater where nomadism is also not very conspicuous (H. & U. KLINGEL, 1966), comparatively long-lasting associations between several rhinos have also been observed.

D. Association between bulls

In Tsavo National Park East we came, in two cases, upon a close association of two bulls. They walked and fed and, in one case, also fled together as an activity unit. However, as one observation was made from helicopter on the Yatta Plateau, and the other from Landrover on a trip to Voi, we have no further information concerning the nature and persistence of these associations.

Finally, it may be mentioned as a matter of interest, that two tame male rhinos, one born in 1960, the other in 1964, live together at Voi Headquarters. Both pass the night in a stable, but are led into the bush every day, together with some immature tame elephants and buffalos. Both rhinos have adopted child rôle towards man and tend to keep together as a social unit in resting, feeding, and moving. As these rhinos are not alarmed by human scent, we do not know how they would react in the case of serious alarm.

III. Non-ritualized behaviour patterns of daily activity

In this chapter a short description is given of daily and frequently observed behaviour patterns, which are not ritualized, i.e. not especially shaped as social signals. This does not mean that they have no such function. On the contrary, they are effective signals in the case of transfer of mood and impulse.

A. Feeding

The normal food items of the black rhino are – as pointed out in Ecology I.B. 1. – small trees, bushes, shrubs, some very low, creeping plants and even occasionally grasses. The feeding technique has to be adapted to the respective type of food plant.

Generally some twigs or stems are seized with the upper lip, pulled and bent, then cut off with the premolars and finally chewed from proximal to distal. Each chewing movement produces a grinding noise which can be heard at a distance of 30 to 40 meters. These chewing movements follow one another in intervals of approx. 1 second. As mentioned (Ecology I.C. 1.), the twigs of a few plants, as e.g. *Bauhinia taitensis*, are too tough to be simply cut off. Cutting is then combined with a twisting and pulling movement of the head. In one case, a female was observed to bend a slender tree down with her first horn by rotating her head and then to feed on the twigs of the small treetop.

B. Drinking

When a rhino has reached the edge of water, it normally remains motionless for several seconds. Then it either drinks from the edge or it steps into the water. Sometimes the lower part of the belly is submerged in the water; in most cases where the animals were sexed, these latter ones were males.

A rhino drinks continuously for 30 sec. to 1 min. 45 sec., then lifts the head for about 10 to 20 sec., the ears upright, surveying the surroundings acoustically. A second phase of drinking follows, and often a third after a short interval. The total time spent by the individual rhino in drinking was on the average 4 to 5 min. with 2 to 3 short interruptions, if undisturbed.

After drinking the rhino leaves the water immediately, but often stops again at a short distance and remains standing motionless.

C. Salt licking

In Amboseli and in Tsavo East where we have observed rhinos systematically, salt does not seem to be in short supply. In both regions *Suaeda monoica* grows near the water and is often browsed by rhinos. This species indicates a comparatively high salt content of the soil, and has a high salt content itself.

In Amboseli we observed a rhino bull licking at the same spot for several minutes. The animal had first removed a thin layer of dried mud with lip and tongue. Then it licked the spot with regular strokes of the tongue, lifted the head, and continued the tongue movements with reduced amplitude. After this, the whole sequence of soil licking and simulated licking was repeated. Eventually, after about 10 min. the bull walked away and started feeding.

In our observation areas in Tsavo and in Amboseli we have not seen special salt licks in use and dug out by generations of rhinos as RITCHIE (1963) and SPINAGE (1960) have reported from the Aberdares.

D. Resting and sleeping

The rôles of resting and sleeping in the daily program have already been outlined (I.B.). In most cases rhinos lie down to rest and sleep. But, also, dozing while standing with lowered head for some minutes and up to an hour was often observed, especially in old bulls or in one member of a mother-child-unit. Mothers often remain dozing near their sleeping baby or calf. But sometimes a mother is lying, while the calf, after having risen and ventured into the vicinity, turns back to its mother and remains there "waiting" and soon dozes next to her.

Behaviour connected with resting and sleeping on dry wallows, other sleeping places, and in ponds or puddles is somewhat different.

1. Dry wallows

When visiting a wallow the animal walks purposefully towards it, sniffs the soil, and turns on the spot with short, dragging steps. Then it lies down, first settling with its hindquarters on one thigh, then going down with the anterior part of the body, and wallows on one side of the body. After lying in normal position for some time – from part of a minute to several minutes – the rhino gets up on its feet, turns on the spot, lies down, and wallows on the other side of the body. Then it remains lying, sometimes for a few minutes completely stretched out on one side, but normally with the hindquarters resting upon one thigh, the anterior part of the body slightly to the same side, the head on its ventral surface (Fig. 15). In this position the rhino may rest and sleep for hours, even when exposed to burning sunshine.

Figure 15. Young cow lying on a wallow.

2. Other sleeping places

When a rhino becomes drowsy in a feeding area with no wallow nearby, it begins to doze while standing, the head hanging down. From time to time it lifts the head, perhaps feeds again at low intensity, and then again begins to doze. It may then sniff the soil while taking small steps and suddenly lift the head, erect the ears examining the surroundings, then lie down in the open. In hot sunshine rhinos often go to a tree or bush and remain at first standing in the shadow. In this case also, the phase of reactivation with lifting of the head and erecting the ears precedes lying down. As at the wallow, the rhino often rises after having lain for some time, feeds perhaps once more, begins to doze again, and after the short phase of reactivation lies down on the other side of the body for a long rest and sleep.

3. Ponds or puddles

In Tsavo National Park East, and especially on the Yatta Plateau there are many small ponds or puddles during the wet season, which dry out regularly during the dry season. In these ponds rhinos often lie for hours (oral communication by D. SHELDRICK). In the course of this study we have seen only three animals sleeping in such a bath; in one case a bull and a cow, in another case a bull alone. In both cases we had no opportunity of observing the procedure of entering the puddle and lying down.

While lying and dozing or sleeping, most rhinos still move the ears in an automatic detection technique: more or less independently, each ear rotates slowly sideways, then with a quick "jump" forwards and again slowly sideways. As soon as a sound or noise is perceived, the ear readjusts in its direction. If the rhino is mildly alarmed by the noise or by tickbirds, it lifts the head; but in most cases of alarm the animal rises at once, with both ears facing in the direction of the alarming noise, – or in the case of alarm by tickbirds – facing in the direction with the wind and focusing in different directions with ears erect.

While lying the rhino also moves its tail in a typical "clumsy" wagging movement. When on a wallow, it throws small clouds of dusty soil over its rump and side with its tail. In some cases a rhino, lying on a wallow, suddenly made a loud sneezing-snorting noise. Most probably dust had entered the animal's nostrils and had elicited sneezing.

E. Mud- and dust-wallowing

Mud- and dust-wallowing are not always a preparatory phase to resting and sleeping. Often a rhino goes to a wallow only to wallow, and immediately or soon afterwards leaves again. Circling on the spot, which regularly precedes dust-wallowing, was not observed as preparation for mud-wallowing.

Wallowing itself consists of one to three rotation impulses by which the animal rolls on one side until all four legs are well off the ground, those of the upper side almost vertically. We never saw a rhino rolling over its back on to the other side. After having reached a maximum elevation of the legs, these fall back again. In most cases, after wallowing on one side, the rhino rises and then wallows the other side.

F. Head- and horn-rubbing

In zoological gardens the black – and also other – rhinos rub their horns frequently on walls, doors, concrete poles etc. In many cases this activity appears stereotyped, occurring as an outlet of a drive or urge which in a normal environmental situation would lead to some kind of appetitive behaviour.

Stereotyped horn-rubbing results in a shortened horn or, better, in a special type of abrasion of the permanently growing horn. In most cases the horns then attain a more or less polygonal shape in transsection.

During all our observations we have seen only one rhino with pronounced marks caused by rubbing of the horns. It was the very old and week cow with completely worn molars, shot on 13th Oct. 1966.

Most of the horns had a smooth surface all around the distal part, a more or less circular shape in transsection and were nicely pointed.

The great variety in the shape of horns is not due to different kinds of abrasion. Only in very few cases was the use of force involved in shaping the horn: in broken horns, in horn stumps and in longitudinally split horns. Further we have never observed any horn-rubbing which might have resulted in a sharpening effect.

Rubbing of the head was observed more frequently; particularly in two situations rhinos were seen to rub the sides of their head and snout and the base of the first horn, on trunks or stumps of trees:

1. At the main watering place bulls were seen to sniff carefully at stumps and then to rub (their head etc.) with repeated up and down movements of small amplitude. It seems that this activity also has a function of scent-marking.
2. A mother with a half-grown calf which we followed, stopped in a small clump of trees. While the calf lay down and suckled, the mother stood first motionless, then rubbed her head etc. on the trunk just in front of her. In this case the activity appeared very similar to horn-rubbing in the zoo: the cow had to wait, and the trunk near her just offered the opportunity for activity.

G. Tail and ear movements without signal function

When walking and feeding, the rhino normally moves the tail sideways up over one side of the rump, then back again and up on the other side. This movement is quite peculiar, "stiff" or clumsy. In most other ungulates an energetic impulse moves the tail like a whip over one side of the rump; then it falls back like a pendulum and just before it reaches the lowest position a new impulse throws it on to the other side. In the rhino there is no sudden initial impulse. The tail is moved upwards by a continuous contraction of lateral muscles and "kept" for a short time in its terminal position. Then it does not fall back with obvious acceleration, but with a somewhat controlled spead, which leads to a stop when the tail has reached the normal vertical position.

We do not know whether this tail movement occurs only as a reaction to flies, or sometimes also as a stereotyped internally released motor pattern. The tail is certainly only effective against flies in a very restricted area around the rump.

Rhinos also flap with the ears; this occurs most frequently when the rhino is lying. Flapping is distinctly different from the normal rotation by which the rhino surveys its surroundings acoustically. Most probably flapping is a reaction to flies: it lacks the regular periodicity of the rotation.

Ear-flapping also occurs when the rhino is on the alert and listens with erect and focusing ears. In some cases it seemed that the rhino was chasing flies in order to be able to listen undisturbedly; in others the rhino chased tickbirds sitting on its head and chirrupping, with head-shaking and ear-flapping.

IV. Reactions to other large animal species and to man

In outlining the ecology of the rhino we have already mentioned those animal species which cause reactions on the part of the rhino and have some ecological importance for the species. The basic reactions of the rhino to man have also been outlined. In this chapter the special behaviour patterns involved in these reactions will be described.

A. Reactions to large mammals and to the ostrich

We have observed seven main types of reaction with variations among them.

1. Loose association with large ungulates

This reaction does not consist of special behaviour patterns. On quite a number of occasions rhinos – single or in twos – were seen in association with a buffalo herd. While the buffalos were grazing, the rhinos were browsing. In case of disturbance the buffalos closed up, while the rhinos took to flight on their own. Association with zebra and oryx was also observed on several occasions, but appeared less harmonious and stable. Presumably the feeding- and moving-style of these ungulates differs more from that of the rhino than does the style of the buffalos.

2. *Alertness-curiosity-reaction*

When coming near to another animal, the rhino often reacts with alertness and curiosity. With the head slightly lifted, the ears upright and focused on the other animal, the rhino remains motionless or takes some steps forward.

3. *Imposing posture*

If the other animal continues to approach, the rhino may lift its head even higher and stand or advance in this posture (Fig. 16). This reaction was most pronounced in the case of subadult lions stalking a male rhino in a playful manner (see Ecology II. A. 1.).

4. *Holding the ground*

This is the normal reaction of a rhino lying on a wallow or on a sleeping place when disturbed by elephants. The reaction shows variations in intensity.

When elephants approach the rhino, it rises and remains motionless with lowered head. If the elephants do not pass by, but remain or even continue to approach, either one of the following two reactions may be observed. The rhino takes one or two steps forward, or one or two steps backwards and then moves forward again. In one case, the rhino took the step forward with its head nearly as high as in alertness, but in other cases the head was slightly lowered. The steps forward may be accompanied by snorting.

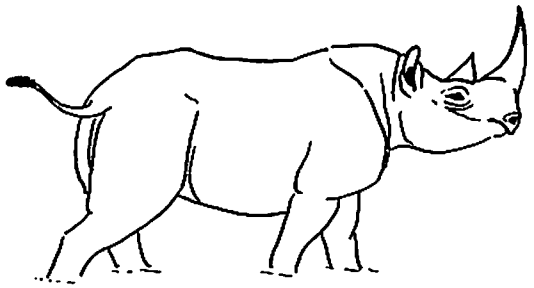

Figure 16. Bull in imposing posture.

Usually, the elephants eventually leave the rhino. In the following scene the two rhinos involved did not succeed in holding their ground, but the elephant chased them away.

Obs. Nr. 8: Two female rhinos, well known to us, most probably mother and daughter, were walking along Simek River swamp in Amboseli Game Reserve. They went to a place with shallow water, overgrown with marsh-grass, wallowed there and lay down, while a bull elephant was feeding on the grass within some 30 meters. The elephant approached slowly while feeding. When he was within 10 mtrs., the rhinos rose. The mother faced him, the daughter stood behind her, facing slightly to the left. Now the elephant also stood motionless for some 10 seconds. But when the mother took two steps forwards, the elephant advanced quickly one large step, lifting his head energetically, and swung his trunk forward into a horizontal position. Both rhinos immediately took to flight and trotted away to a distance of about 60 meters.

5. *Aggressive rush*

This reaction of the rhino reveals its intention of chasing another animal away. We have observed it in two types of situation, and a third one has been reported.

a. When a rhino has been alarmed by tickbirds, and simultaneously a zebra, antelope or warthog suddenly moves nearby, the rhino may chase this animal over a short distance, before trying to locate the human disturber. The same reaction was observed when the first alarm was given by those ungulates. The rhino was also startled, and chased a zebra or antelope passing nearby, then tried to locate us. This reaction might be classified as "redirected defensive aggression". In the sudden excitement of the alarm situation the rhino simply attacks whatever is moving nearby. It may be mentioned here that zebra and especially oryx often react in a special way upon man when a not yet alarmed rhino is near: they tend to move in such a way that the rhino is between them and the human disturber, and then wait and watch the situation.

b. In a number of cases rhino bulls rushed at a waterbuck, an impala or a zebra which was simply in their way. The motivation of these attacks is difficult to interpret. They did not seem to be play activity. The rhino appeared to be disturbed or irritated by the other animal nearby, and therefore reacted with aggression.

c. It has been reported by several observers that in defending a waterhole – especially in the case of scarcity of watering places – or at a saltlick, rhinos sometimes rush at elephants or buffalos with an agressive puff or snort, in order to chase them off. In our study area we had no opportunity of observing interspecific competition of this kind.

6. *Dodging with easy canter*

Rhinos sometimes avoid conflict with elephants by trotting leisurely out of their immediate reach. The following observation may illustrate this type of reaction:

Obs. Nr. 9: A rhino bull in following a main track to the water overtook a slowly moving family-unit of elephants by changing to a parallel secondary track. Some subadult elephants turned in his direction, spread their ears and walked towards him in a playful attack. The rhino quickened its gait to an easy canter, while two of the elephants indulged in playful pursuit, but only for a few seconds. As soon as the rhino had passed the elephant group, it slowed down to the previous steady pace and changed back to the main track.

7. *Flight*

On two occasions rhinos were seen to take to flight in the course of an encounter with another animal:

- A bull approached a group of ostriches, most probably expecting to meet another rhino. When he was close enough he suddenly ran off, first in a gallop with his tail up, then with a speedy trot (see Ecology III. C. 2.).
- Two female rhinos ran off when a bull elephant advanced with his ears spread and his trunk swinging forward, as described in Obs. Nr. 8.

In a few other cases a small calf venturing around its mother was frightened by an antelope and ran back to its mother. Flight released by another large animal resembles flight caused by man, when human scent is not involved. Flight as a reaction to human scent is usually of higher intensity.

B. Reactions to man

The most striking feature of these reactions is their enormous variability and apparent nonpredictability. But in trying to analyse them we will find that some main factors which shape them can be recognized.

One of these factors is local tradition. In different local rhino populations, the disposition to react to stimulation by man is very different. Most probably these local traditions are transferred from mother to child.

There is no doubt that individual experiences with man also basically influence the type of reactivity in the presence of man. Rhinos which have been wounded are said to be more inclined to attack man than others.

Fully adult bulls usually appear more self-confident than subadults or cows. Mothers with calves show a strong tendency to take to flight. The type of stimulus by man is also very important for the type of reaction in rhino. But, admittedly, the many encounters we had with rhinos show many special characteristics, not all of which we are able to analyse.

In a very general way, all the reactions reveal that a rather small number of tendencies are involved in varying proportions:

- a tendency to investigate = "curiosity"
- a tendency to avoid man or to flee = "fear"
- an aggressive tendency = "anger"
- a tendency to limit the effort = "inertia"

In the following description of reactions to man we refer mainly to our own observations in the Galana-Yatta Region of Tsavo National Park East and only in a few cases to experiencies which we had with rhinos in other regions (Amboseli, Manyara, Ngorongoro, Mara, Nairobi).

We differentiate between encounters with man on foot, in a car, in a low flying aircraft; in addition, in accordance to the type of initial stimulus by man which elicited the first reaction of the rhino:

- olfactory stimulation
- tickbird alarm
- acoustical stimulation
- stimulation by the sight of man.

In many encounters it was clearly one of these stimulus categories which caused the first response by the rhino, but often in the course of the encounter different stimuli became effective, and the reaction of the rhino was an integrated response to the complex situation. In some cases, however, it was evident that the reaction to one stimulus blocked the response to other stimuli also present in the situation.

1. Reactions to man on foot

a. Human scent as initial stimulus

Human scent elicits reactions in the rhino if carried by air or if adhering to human footprints, thus forming a scent track. Rhinos react differently to scent tracks of different age, and when they receive human scent in the air, the distance between man and rhino and properties of air movement are important factors. If alarm of a low degree is elicited by human scent in the air, the rhino remains on the spot, the tail slightly raised. When the wind is unsteady in its direction, the up and down movement of the tail is an indicator of changing excitement in the rhino. The nostrils are wide open, and while the rhino carefully checks the air, the upper lip has an extremely wrinkled appearance (Fig. 17), and sometimes almost adopts a shape as in "Flehmen"[4] – only head and nose are not lifted correspondingly.

[4] "Flehmen" (SCHNEIDER 1930) in the rhino: the animal lifts its head, the nose pointed upwards, it stretches the upper lip forwards-upwards, so that the downward bend of the tip disappears completely and the shape of the nostrils is changed. "Flehmen" is widespread among ungulates, but occurs in the lion and the tiger as well. Its function is chemoreceptory testing.

Figure 17. Cow, taking scent.

Sometimes – especially if the wind changes constantly and only traces of human scent reach the rhino from time to time – it may face against the wind with ears erect. It will often remain in this position in the cover of bush vegetation, on the alert over a considerable period of time.

A human scent track produced one to three hours before the rhino comes upon it, will also elicit alarm of low intensity. The rhino may sniff the soil, then lift the head with ears erect while the tail is also lifted. Over a short period e.g. some seconds, the apprehensive tension in the animal may go up and down, as shown by the style of walking, the degree of alertness, and the position of the tail. Then, after it has crossed the track, the rhino usually soon quietens down.

In alarm situation of a higher degree induced by human scent in the air, the rhino will take to flight. In the Galana-Yatta Region the wind often blows steadily from the south during the dry season. Under these circumstances, rhinos downwind of man reacted with flight at a distance of 800 mtrs. to 1 km. The first phase of flight is usually a powerful gallop over a distance of 30 to 150 mtrs.; then the animal changes to a speedy trot. During the whole of the flight the tail is held vertically at its base and often curved forwards at its distal part (Fig. 18). If man is very near to the rhino when it receives his scent, the chance is greater that the rhino will not flee over a long distance. On the other hand, when the rhino catches the scent of a man several hundred meters away, it will not stop its flight soon. This is most probably because in the first situation the rhino has a greater chance of getting out of the range of human scent, while in the second case the "infestation" of the air around the rhino is less localized. A very short flight caused by scent in the air may extend over 150 to 200 mtrs., a long one over more than 1 km. Once a flight of over 3 kms was observed. The angle between the direction of the flight and that of the wind differs from case to case, and is by no means a stable characteristic of the flight. It seems rather that the fleeing rhino goes towards an area where, by experience, it can expect to remain undisturbed. This is often the area from which the rhino has just

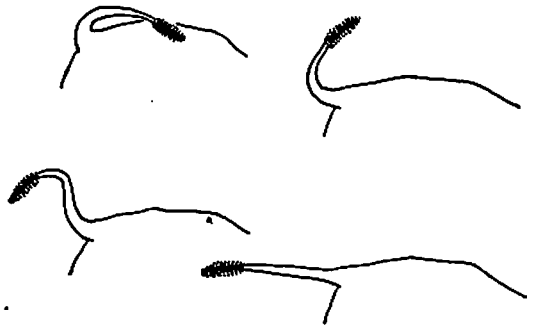

Figure 18. Tail up in flight; different postures.

Figure 19. Fan posture of three rhinos when stopping in alarm excitement.

come. Rhinos which were disturbed near a driving track fled away from the track. When reached by human scent in a comparatively open flat on the foot of the Yatta Plateau, they often fled up the slopes and on to the Plateau. Very often the flight was through comparatively dense bush. After a flight of 150 to 300 mtrs. a rhino often stops in bush cover, turns around to the left and to the right, with its head lifted and ears erect in order to check the situation with ears and nose, facing with the wind. When two to four rhinos have fled together they adopt fan position after stopping (Fig. 19). If after a short flight the stop is definitive, the posture of watchfulness may be maintained over some few to 10 or more minutes. Usually after a stop of some seconds, flight is continued. In a number of instances a short stop was combined with defecation. The dung was dropped without making use of a "lavatory" and scraping was absent or was very short and hasty. Mother and calf, or bull and cow occasionally defecated simultaneously. After defecation the animals continued on their way with reduced speed and soon calmed down. Evidently defecation took place at the moment of a marked decrease of fear or flight excitement.

In the course of a long flight, the rhino sometimes changes from trotting to walking, especially while climbing a slope, but later trotting may be resumed. When the flight comes to an end, which normally happens in bush cover, the rhino will again face in the direction of the wind, head up, ears erect; if there is more than one individual, they will adopt fan position. Where bush vegetation reaches only to the rhino's withers, it will lift its head to this level and sometimes turn it to the left and to the right at irregular intervals. This head-swivelling was more frequently observed in Amboseli than in the Galana-Yatta Region. After intense and long flight, rhinos may stand in bush, still on the alert, for half an hour and even more.

Alarm of higher degree caused by a fresh human scent track also releases flight. Normally flight is preceeded by the following sequence of reactions: sniffing – lifting the tail – uttering a short puffing snort once or twice, and simultaneously rushing forward with lowered head (Fig. 20) for 5 to 10 mtrs. The rush, which may be called a blind defensive aggression, is usually followed by flight. Sometimes, however, the rhino stops, sniffs the soil again while making some

"nervous" steps, performs another rush with or without puffing, and eventually takes to flight.

Generally flight caused by fresh human scent tracks shows the same features as flight caused by human scent in the air. Both stimuli may act together, especilly if at the moment of alarm, man is still near. In this situation yet another sequence of alarm behaviour has been observed: when perceiving human scent, the rhino first produces the short snorts with or without a short rush, then stands in imposing posture and utters a "long snort" which sounds like a prolonged German "rrrrrr..." produced with the tip of the tongue combined with hissing expiration.

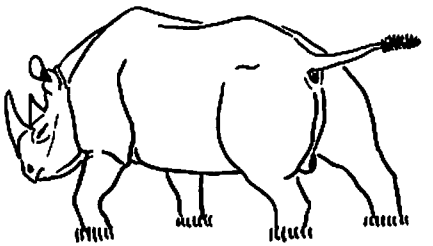

Figure 20. After sniffing a fresh human track, a bull rushes forward, snorting and with his head lowered, in "blind defensive aggression"; then he takes to flight.

In the study area all categories of rhinos take to flight when reached by human scent not combined with acoustical or optical stimulation. In the case of combined stimulation there is much greater variation and nonpredictability of response.

b. Alarm chirrup of oxpeckers as initial stimulus

The reactions of rhinos to the screeching of oxpeckers also show many variations, not only with regard to intensity, but also to quality. The components of fear (or a tendency to flee), aggressiveness (tendency to defensive or aggressive attack), and inertia appear in different proportions. The tendency to investigate is often very pronounced, sometimes in the sense of inquisitive attention, sometimes of exploratory activity.

One cause of the variability in the response of the rhino lies in differing types of alarm behaviour of the birds. Occasionally they fly off immediately after chirping, thus causing alarm in the rhino during one moment only. In other cases they screech, climb on top of the rhino's head and back, remain in alarm posture and screech again and again without flying off.

Obviously fear is predominant, if alarm by the oxpeckers makes a lying rhino rise and take to flight immediately. Inertia prevails over fear in the following cases:

Obs. Nr. 10: A mother with calf sleep on a wallow. When we approach them carefully downwind, some oxpeckers chirp and immediately fly off. The rhinos move their ears more intensely for some seconds, but do not show any further reaction.

Obs. Nr. 11: In another similar case, two rhinos lifted their heads, erected their ears and opened their eyes, but after two minutes they dozed again and soon fell asleep.

Obs. Nr. 12: A subadult female was lying beneath a thornbush when we approached. When the oxpeckers screeched, she rose and stepped out of cover, lifted head and tail and erected her ears in attention. As we continued to approach carefully, the birds flew off. The rhino remained motionless on the alert, but as we caused no further disturbance, she soon relaxed and became increasingly drowsy. Suddenly she lifted head and ears once more; but it was the normal phase of reactivation before lying down. She turned on the spot, sniffed the soil, took a few steps and lay down again.

In similar reaction sequences mother-child-units always form the "fan" in the phase of full attention.

Obviously in these scenes the reaction is not characterised by an arousal of fear and flight. The first phase of the response is alertness or – even better – inquisitive attention. It is a preliminary reaction and leads, in the cases described, to a final response: to relaxing completely and resting or sleeping. Not all responses to the screeching of tickbirds form a sequence of the two components, inquisitiveness and final response. The following examples show a more complicated structure:

Obs. Nr. 13: We approached a single subadult bull who was walking slowly through scattered bush and feeding with low intensity. Upon the screeching of "his" oxpeckers he turned around, fully on the alert. In a seemingly hesitant way he turned and trotted off around the next group of bushes. There he stopped, turned again, and stepped forward until his head, breast, and forelegs were no longer hidden behind the bush, and again stood fully attentive. After several seconds he again turned and trotted off for a short distance; but as we did not follow him, he soon relaxed and continued his walk.

Obs. Nr 14: A mother with calf following a game track came in our direction. We climbed a termite hill and remained on its top in crouched position in order to take some photos. When the rhinos were about 35 mtrs. away, the tickbirds screeched. Mother and calf lifted their tails immediately and advanced with ears turned in our direction. When the oxpeckers chirped again, the rhinos changed their direction somewhat to the right. As the birds were now silent, the rhinos lowered their tails but were still on the alert, and the oxpeckers sat on their backs in alarm posture. The track which the animals followed now ran about 20 mtrs. from the termite hill. While the rhinos advanced, the birds screeched once more and immediately tails and heads of the rhinos went up and their ears focused in different directions. When they had gone by, the birds quietened down and the rhinos who had not been reached by our scent during the whole encounter, continued to move, but now in a relaxed manner.

Obs. Nr. 15: We approached a mother standing in the shade of a tree with a small calf lying near her. After the screeching of the oxpeckers, the cow lowered her head and performed a single symbolized stab with the horn (= symbolized horning). After that she remained on the spot at full attention, head and ears upright. Then she repeated the symbolized horning. As we left, she followed our movement with her ears and became more and more relaxed.

Obs. Nr. 16: In a small valley with scanty bush vegetation we approached a bull who fed on the opposite slope. When we were at about 60 mtrs. from him, the tickbirds chirped. The bull became considerably excited, he listened in our direction with head and tail up, then showed symbolized horning, trotted off for 15 mtrs., stopped, turned around, and listened again in our direction. As we approached carefully, the oxpeckers screeched again and the bull shook his head, flapped his ears, and stamped with his hindlegs, obviously with the intention of getting rid of the noisy birds. Then he trotted off for some 20 meters. Partially hidden in low growing shrubs, he turned around, listened, then scraped vigorously, defecated and scraped once more with equal intensity. Eventually he trotted off in a peculiar manner: he did not follow exactly the direction away from the disturber, but deviated to the right over a short distance and then to the left alternately, and emphasized each deviation by turning his head to the respective side (Fig. 21). The same flight pattern was observed in eland. Presumably it has to be interpreted as a technique by which the animal can detect whether or not it is pursued.

Obs. Nr. 17: We approached a bull downwind. He was loosely associated with a small cow who was feeding intensely some 30 mtrs. away. When we were about 40 mtrs. away, the bull was alarmed by his tickbirds. He scrutinized, performed symbolized horning, scrutinized again, then stepped forward, stopped, repeated

the symbolized horning and was again fully attentive. Twice more he advanced and repeated the symbolized horning, but as we kept extremely silent, his tension eventually decreased.

Responses of this character are usually explained by conflicting tendencies, but this interpretation risks overlooking their important "instrumental" properties. One of these properties which we have discussed already is inquisitive attention as a preliminary or preparatory reaction. Obviously the phase of inquisitiveness does not always lead to a final action, but in many cases to behaviour sequences containing initial movements of final actions which themselves alternate with renewed inquisitive attention. These movements may be interpreted as intention movements (Intentionsbewegungen).

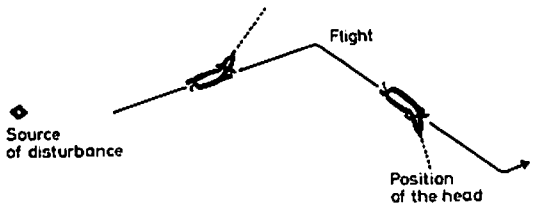

Figure 21. Flight pattern with changing direction.

In the above mentioned observations the sequences appear as:

Obs. Nr. 13: – inquisitiveness – flight intention movements – inquisitiveness – flight intention movements – quiescence

Obs. Nr. 14: – inquisitiveness – quiescence – inquisitiveness – change in direction – inquisitiveness – quiescence (moving)

Obs. Nr. 15: – inquisitiveness – attack intention movements (weak threat) – inquisitiveness – weak threat – inquisitiveness

Obs. Nr. 16: – inquisitiveness – weak threat – flight intention movements – inquisitiveness – flight intention movements – "excited" defecation – flight

Obs. Nr. 17: – inquisitiveness – weak threat – inquisitiveness – threat of higher intensity – inquisitiveness – threat of higher intensity – inquisitiveness – threat of higher intensity – inquisitiveness – quiescence

What we called intention movements of final acts are actively exploratory or path-finding components of the response sequence. During this phase the rhino is no longer the receptor only, as in the first phase of inquisitive attention, but an exploring actor. The response as a whole is far from being an automatic, reflex-like, behaviourial unit. It is rather the active "feeling out" of the situation which prepares the possible final situation or act, quiescence, flight, or attack. The entire reaction could generally be outlined as follows:

Inquisitive phase – phase of exploratory tactics with intention movements of final acts and inquisitiveness in alternation – final act or quiescence.

In some cases however, rhinos responded immediately with a final act upon the alarm call of the oxpeckers, namely with flight. In all these cases the rhinos had been lying; they were taken unaware. In a situation of real danger from man, e.g. from hunters with poisoned arrows, immediate flight may have survival value indeed. The following observation shows such immediate flight:

Obs. Nr. 18: A rhino cow lying in low growing shrub was alarmed by oxpeckers when the observer was about 30 mtrs. away. She rose and happened to run in full speed in his direction. He moved sideways hoping to be able to get out of the way. The rhino saw him move at a distance of 12 to 15 mtrs., changed direction and ran off. Here flight obviously had a quality of adaptation to the actual situation.

So far we have not described any encounter in which tickbird alarm provoked a real attack by the rhino.

Gestures of threat will hardly ever lead to an attack without an appropriate optical stimulus to guide it. Even if the threatening rhino can see a man, it might still perform a bluff attack only, that is rush at him, stop suddenly, and turn off.

Obs. Nr. 19: In one case, however, one of the authors approached a rhino bull on an open flat slope. When at a distance of 40 to 50 mtrs., the bull was alarmed by oxpeckers and could obviously see the disturber as a moving silhouette against the evening sky. He charged at full speed. The author ran towards him shouting, hoping that the rhino would be frightened. But this did not happen. So he avoided the bull by swerving, passed him, and made for a small tree 20 to 30 mtrs. further away. The rhino turned immediately and despite the fact that human scent had now reached him, chased the author. After a chase which led several times around the small tree whose main branch with its top had been broken down by elephants, the author finally tried to climb into the branches. But he was reached and thrown up by the rhino. He fell down first on the rhino's shoulders, then onto the ground and hid under the broken down and dead treetop. But the rhino pushed away this part of the tree which was still attached to the living main trunk. The author, lacking any protection, remained lying on one side with one leg lifted, intending if necessary to push himself off the rhino's nose. The rhino indeed approached until his nose touched the author's foot, then made another small step forward while the author gave way by flexing the leg. Then, suddenly, the bull lifted head and tail and trotted off in the zigzag flight described above (Obs. Nr. 16). Obviously, when optical stimulation by the running human figure ceased, the olfactory stimulation became effective and caused flight in the way traditional to the rhinos in the Galana-Yatta Region.

c. Reactions of rhinos stimulated acoustically by man

As has been pointed out (Ecology II. A. 2.) rhinos have an acute sense of hearing. When man approaches a rhino carefully, ear movements often reveal that it hears the observer from appr. 40 to 60 meters. But in most such cases, their reactions do not indicate that they are immediately seriously alarmed. As with alarm by oxpeckers, there is great variation in these reactions. Sex, age and association are important; the locality of the encounter and the type of noise made by man contribute to determine the reactions, and undoubtedly local and "family" tradition, individual experience, and the actual mood of the rhino are also involved. As long as man produces noise in walking at a distance of 60 mtrs. and more, the rhino's reaction varies between occasional listening and more intense acoustical surveying. If the observer now goes further away, the rhino will follow with the ears, but will then soon lose interest. But when the disturbance comes closer, the rhino will rise and focus its ears upon the source of noise. Investigation may be more pronounced in such situations than in the case of alarm by tickbirds, while the component of fear or suspicion is less prominent.

The following observations show clearly these components of the response:

Obs. Nr. 20: We approached a mother when she was suckling her nearly half grown calf lying beneath her. When the calf had finished suckling, the mother started to move, and the calf quickly rose and followed her. We filmed this scene at a distance of approx. 30 to 40 mtrs. The cow obviously heard the noise of the camera, faced in our direction with her ears focused on us, and came walking towards us without any sign of fear or threat. We disappeared behind the nearest thornbush, and as the rhinos still advanced, went further back, one of us to the right, and the other to the left, in order to find cover behind some small bushes. The two rhinos still advanced, the mother leading with ears focused now to the left, then to the right. She crossed our footprints, but did not take any notice of the scent. First she turned to the left, then to the right. When she was within 5 mtrs. of one of us, this one ran away and the other shouted; at this moment the mother seemed to sniff the air and was now fully alarmed. Within a second, mother and calf ran off first at full gallop, then at a trot.

Obs. Nr. 21: While standing in the forks of a tree the top of which had been broken of, we observed a mother with baby. The animals had been moving slowly in our direction, the mother feeding here and there on the way. When 15 mtrs. from our observation tree, mother and baby lay on a wallow and the baby licked the rain water which ran down its mother's flanks. Remaining motionless became increasingly painful and we had to change our positions from time to time. Each time the mother lifted head and ears, but did not seem to have any intentions of leaving. As after a time we had to leave anyway, and there was no hope of getting down from the tree without disturbing the rhinos seriously, we decided to disturb them while we were still in the tree. When we shouted she rose together with the baby and came slowly in our direction. We shouted again and she continued to advance. When at a distance of 6 mtrs., she seemed to discover our position in the tree and moved somewhat sideways around it. We finally shouted at her as loud as we could, which resulted in her turning off, tail lifted. At this moment three warthogs ran by at some 20 meters. This stimulated the cow to rush in their direction in a short bluff attack, the baby behind her. But then she was reached by our scent and she and her baby really took to flight.

In both cases the tension of suspicion which characterizes inquisitive attention and exploratory activity in the case of tickbird alarm, was not present during the first phases of the reactions described. Especially in the first example our impression was that the mother (who with her calf were the only rhinos in the area) was interested in meeting another rhino. In the second case, a note of uneasiness became more and more apparent in the reactions of the mother.

The following observation may show that, when taken unawares by sudden noise from very near, rhinos may react immediately by flight. Under these circumstances the tendency to take up social contact or to investigate is not activated. As will be discussed later, this is also true in the case of sudden interference by another rhino.

Obs. Nr. 22: A mother and calf came in our direction, moving and browsing. When they were about 6 mtrs. away we called them from behind a tree. Both immediately lifted their heads and focused their ears upon us, then turned and ran off in the direction from which they had come. But they soon stopped and came by a parallel route thus maintaining their general direction, but avoiding the spot where they had been disturbed.

The tendency to take up intraspecific contact can be aroused in bulls by imitating the calls, snorts, puffs and the stamping made by the cow on heat. The quality of the imitation is probably not very important. It is rather the uninhibited acoustical display, unusual in rhino habitat, which has this stimulating effect. But again the response of bulls is far from uniform – as is illustrated by the following observations:

Obs. Nr. 23: A bull lay between shrubs. When we called him from 60 mtrs., he rose and focused his ears upon us. After repeated calls, he slowly walked away through an area covered with bush.

Obs. Nr. 24: A bull was walking in our direction, following a strip of secondary tracks while feeding occasionally. We called him from 50 mtrs. away. With his head up, he listened in our direction. When we called him again, he turned somewhat to the left and continued to move slowly. When passing a bush, he squirted urine onto it, then continued his way, making a detour of approx. 100 mtrs. radius around us.

Obs. Nr. 25: While sitting in a tree we called a feeding bull from 50 mtrs. He at once lifted his head and faced us. After having called repeatedly, he came slowly in our direction. When he was about 10 mtrs. from our tree, we called again in a low voice. He immediately lowered his head, thus adopting a posture of readiness to attack, then went slowly around the tree maintaining the distance. At the next sound we produced, he rushed forward some steps with lowered head. Then, after remaining on the spot for some seconds, he walked backwards scraping vigorously with both hindlegs alternately, and again waited, facing in our direction. Repeated shouting only caused him to go further around the tree and maintain a distance of approx. 15 mtrs. Then he scraped again vigorously. He was now downwind, but did not react with flight. After about 5 more minutes he withdrew slowly and faced in our direction from appr. 50–60 mtrs. until we finally left.

Obs. Nr. 26: Also whilst sitting in a tree we called another bull who fed about 50 mtrs. from us. He lifted his head and turned it somewhat in our direction, then continued to feed. We called him repeatedly, but he did not lift his head again and apparently paid no attention to our calling. However, after perhaps 2 minutes, and without having been called again, he stopped feeding and walked towards us in a curve. In passing near a small bush he squirted urine onto it, then advanced slowly, not exactly in our direction. At about 30 meters from us, he stopped and scraped vigorously, then continued to approach. At a distance of 6 mtrs. from our tree he stopped again and listened to the noise of the film camera. As we involuntarily made a little noise in the branches, he faced, with a jerk, in the direction of the noise immediately lowering his head. Then he went slowly around the tree, while we tried not to make any noise. The moment he perceived our scent he snorted, turned on the spot with lowered head, and rushed off first at a gallop and then at a trot.

Obs. Nr. 27: A family-unit of elephants which we had followed on its way through bush country had reached a termite hill with a rhino wallow nearby. A bull was resting on this wallow. He immediately rose and stood motionless, while the elephants passed him to the left and right, keeping about 4–5 mtrs. away. We now called him from a tree. He faced in our direction and without further delay trotted towards us, passed near the trunk of our tree, got our scent, snorted and ran off.

Obs. Nr. 28: We called a bull who was feeding in low growing bush while an African guide was about 30 mtrs. to our right and perhaps 30 mtrs. further away from the bull. The bull reacted by facing in our direction, and at this moment the guide walked towards us. The bull saw the moving man at a distance of almost 60 mtrs. and immediately faced in his direction. We signalled inconspicuously to the guide to hide. After he had disappeared, the bull again faced in our direction and advanced steadily. We remained motionless on the ground, in the top of a fallen dead tree. The bull, facing in our direction, walked around the dead branches. As he perceived our scent, he snorted performing a short bluff attack, and then ran off.

Bulls lacking self-confidence, avoid an encounter; those who approach upon calling are prepared to fight a rival and presumably to court a cow. Suspicion may grow if the encounter does not develop as it usually does with other rhinos.

d. Reactions to initial optical stimulation

We do not think that in any encounter of rhinos with man on foot, a rhino was first stimulated optically by the appearance of the human. For obvious reasons the observers were not very keen on arranging such a situation. No doubt, the rhino has very poor eyesight compared with other ungulates as e.g. zebra, giraffe, antelopes. Correspondingly it is not by sight that rhinos first become aware of other animals or man. In the course of an encounter however, optical stimulation can play a very important rôle as some of the above described observations show.

Concluding remarks

Man on foot releases alarm excitement of different intensity according to the sensory organs involved. The most important stimulus situations may be compared briefly:

a. In the study area human scent without any acoustical or optical manifestation of man causes alarm of the highest intensity in the rhino. It will flee with great speed for several hundred meters. If the rhino is able to localise the disturber to some extent, it is less frightened than when stimulated by human scent only.

b. When alarmed by screeching oxpeckers, the rhino's reaction is immediate flight only in exceptional cases. Mostly it will face in the direction of the wind, lift its head and investigate the situation mainly acoustically with marked suspicion. After this phase of inquisitive attention the rhino may relax or it shows intention movements of flight or attack, which are suddenly stopped, whereupon it shows again inquisitive attention. We call this phase of the response the phase of exploratory activity. It leads finally to relaxation or to one of two final acts: flight or attack. The last mentioned reaction will hardly occur if the rhino is not very self-confident and cannot locate the disturber with its eyes.

c. The reactions of rhinos to acoustical stimulation by man are in many cases not characterised by fear or suspicion if the distance between rhino and man is not less than 30 to 40 meters. On the contrary, the untroubled investigation by the rhino often reveals its tendency to take up intraspecific contact. When doing so, cows are not aggressively motivated, while bulls are ready to face an opponent, especially when enticed by imitated calls of a cow on heat.

d. It is practically impossible that the first stimulus acting upon a rhino in an encounter with man should be an optical one. When remaining motionless, man will be noticed optically by the rhino only when his shape contrasts with his surroundings. A rhino will optically perceive a moving man at a distance of up to 60 meters, but only when its attention has been aroused previously by other stimuli.

In the case of combined stimulation some of the reactions may appear in concurrence, but in some cases the reaction upon one stimulus blocks another reaction though the appropriate stimulus is also present. In the case of an aroused tendency to take up social contact, scent is most frequently blocked out, and when aggressiveness prevails, optical stimulation may be exclusively effective in directing the attack.

2. Reactions to man in car

The reactions of rhinos to man in a car vary between unconcern, flight and attack. The initial stimulus can obviously be olfactory, acoustical, or optical; in addition the car can appear standing with switched off or with running engine or while moving with varying speed, and may produce a varying noise. But these differences in the stimulus situation cannot account for all of the diversity in the reactions of rhinos. We have to consider that it is only a few decades, in many places only some years, since rhinos first came into contact with cars. Therefore the question arises which factors have contributed and still contribute to shape these reactions.

First it should be pointed out that different types of individual reactions can occur in the same area. In Amboseli Game Reserve two of the ten individuals which we have observed most frequently were extremely shy. These were a solitary female and a solitary subadult animal. Of the other four females, one was easily excited, one

inclined to walk away without hurrying, and the remaining two, most probably mother and daughter, took no notice of cars if these did not come too close, and if the oxpeckers did not screech. Of the four bulls which were observed regularly in the same area, only one showed clearly and regularly the tendency to walk away from cars. The remaining three reacted to cars only if these were too close or were to approach in a careless manner.

Apart from individual pecularities, some characteristics of the actual situation were definitely or most probably responsible for modifications of the actual reaction, as shown in the following observations.

a. The screeching of oxpeckers

Obs. Nr. 29: We observed the two females mentioned above, who are probably mother and daughter, and the young bull who is most probably the son of the older female, when they came to water. After drinking and wallowing in shallow muddy water, they went to a sandy place, lay down there, and slept. We had followed them continuously by car at a distance of 15 to 25 mtrs. and were 15 mtrs. away when they settled down. While they were sleeping one of us carefully opened one door of the car; this elicited no reaction. So he stood to take a photo of the sleeping group. This provoked the alarm call of the oxpeckers, whereupon all three rhinos rose immediately. They remained motionless for one second, then started, almost in the direction of our car and ran past us into a thicket of low growing bush. There they stopped, turned around, and in fan position, the heads just above the bush level, faced in the direction from which they had come. Sometimes they swivelled their heads sideways.

b. Association of the rhino

Obs. Nr. 30: The young bull mentioned above was sometimes alone. Once we found him licking a salty spot on the soil for several minutes. When he had finished, he started to browse. During all this time he took no notice of our car, though we were only 10 mtrs. away.

On another day we found him together with the two cows when a car drove up to them. While the cows appeared relaxed, he displayed a slightly aggressive excitement. With his tail raised in horizontal position, head up, ears erect, he turned in the direction of the car. When another car arrived, he rushed at this one in a harmless bluff attack. Obviously he had adopted the protective rôle characteristic of bulls when associated with females. Possibly the sudden approach of one car after another had also contributed to eliciting the bull's aggressive excitement.

c. The manner of approach

Obs. Nr. 31: A heavy longhorned bull was sometimes in the company of the two cows mentioned above, and a third, apparently young cow also joined them on several occasions, whereas the young bull was alone, obviously avoiding the older one.

One morning the heavy longhorned bull and the three cows lay close together in the sunshine. We had parked our car 40 mtrs. away in the shade of a tree and were not noticed by the rhinos. About 10 o'clock visitors to the Reserve drove up to the group repeatedly. The young cow was the first to show excitement. While the others still remained lying, she rose and lifted tail, head and ears. When more cars had arrived the bull also rose and soon the other two cows also. These two headed for our tree, obviously in search of shade and the young cow and the bull followed them. We backed slowly so as not to disturb them, but when they had almost reached the shade, three cars drove up carelessly. This prevented the rhinos from settling down. The two leading cows walked out of the shade in our direction, while the bull faced one of the cars, stepped forwards, then stopped, and after an instant followed the cows. The cows passed at a distance of 5 to 7 mtrs. from our car. Two faced us for a while but then ignored us. Then the bull came and faced our Landrover. When he began walking towards us and was within 4 mtrs. we started the engine. This apparently stimulated him to threaten: he suddenly lowered his head and made three quick forward steps, while uttering a short aggressive snort. As we reversed slowly, the bull repeated his bluff attack. We now stopped with his first horn 1 mtr. in front of the car, and he remained there for several seconds. Then he passed us at close quarters and followed the cows.

Obviously the arrival of cars had prevented the cows from settling and had caused the aggressive mood in the bull.

Obs. Nr. 32: One evening, when driving in the direction of the Simek River swamp, we found the young bull in front of us walking on the same track and in the same direction. As we approached him from behind, he began to trot. We now left the track and passed him, but he still trotted for a while, obviously disquieted by having been followed from behind.

In our study area in Tsavo National Park East it would have been difficult to observe systematically known individuals in regard to their reactions to man in a car. But our many encounters revealed some other important facts concerning these reactions; the most impressive is the evidence of local habits and traditions.

When driving along the road north of the Yatta Plateau which leads to Malindi we were quite regularly chased by rhino bulls. Several individuals had adopted this habit, probably because they had found by experience that cars after first advancing towards them, always "took to flight", which made chasing them a successful and satisfying activity.

Obs. Nr. 33: One night we left the Landrover parked about 1–2 kms south of this road with several African rangers camping on a rocky hill about 200 mtrs. away. According to their report a bull came along the main track at about 10 o'clock at night. He suddenly noticed the car, rushed at it and attacked it with his horn. He damaged the right metal door with several vigorous horn thrusts so that it hung down on one hinge, looking like wrinkled cardboard. Then he pushed several holes into the side of the body of the Landrover, and finally slit the tyre of the rearwheel and went away.

We had left our Landrover parked overnight in the open in several places south of the Yatta Plateau, but it had never been attacked while parked. Perhaps chasing cars regularly and attacking a standing car are caused by the same motivation: in this area cars have for some bulls the conditioned stimulus value of a gratifying object of aggression.

In the whole Galana-Yatta Region mothers with calves are always alarmed when a car is within 30 meters. Threat behaviour by the mothers followed by flight or simply flight are the usual reactions. Single females are also easily alarmed. Generally the rhinos of the Galana-Yatta Region react much more intensely to cars than do most of the Amboseli rhinos. Some types of frequent reactions which have not yet been mentioned, are described in the following observations:

Obs. Nr. 34: We tried to approach a subadult single bull by driving carefully through scanty bush vegetation. The bull did not really face us, but merely kept one ear turned in our direction, and walked farther away when we were within 25 meters. This reaction occurred repeatedly as we tried to approach again.

Obs. Nr. 35: As we followed a track along a small valley, we met an old bull feeding 15 mtrs. from the track. He stood approx. parallel to the car, lifted his head without facing us, and, slightly raising his tail, walked away from the track.

Obs. Nr. 36: When driving on a track over the Yatta Plateau, we came upon three rhinos, a bull and two cows. The animals were alarmed and, with tails up, they trotted more or less parallel to the track, but not one behind the other as mother and calf would do. Soon the cows turned away from the track while the bull crossed in front of us – a well known reaction of many rapid runners among plant-eating mammals and birds. After having crossed, he trotted more or less parallel to the road for a while, then turned off from the driving track.

Obs. Nr. 37: A young bull near the track on which we were driving, trotted away with the tail lifted; he went into a bush thicket, turned around, and listened.

Obs. Nr. 38: An old bull was feeding 40 mtrs. away from the track on which we were driving. As we stopped without switching off the engine, he seemed to take no notice of us. He left the bush where he had been feeding and walked first in our direction, then parallel to our track. Suddenly, without facing us and without changing direction, he performed a short symbolic attack, rushing forward for some steps with his head lowered. Then he changed direction and, without speeding up, walked further away from the track.

Obs. Nr. 39: Coming from the Yatta Plateau we were driving on a track in the direction of the Galana River, when we saw a bull about 50 mtrs. away and some 20 mtrs. off the track. An instant later the bull had turned in our direction lifting head and ears, and when we were 30 mtrs. from him, he broke into a trot, clearly heading towards the moving car. We stopped, but by pressing slightly on the gas pedal, increased the noise of the engine. The bull also stopped, then turned and trotted off with his tail lifted.

Obs. Nr. 40: In a similar case, a bull withdrew for some 20 mtrs. only and then faced us again.

Obs. Nr. 41: Driving through bush we suddenly found a bull and a cow 20 mtrs. in front of us. They faced us, then the bull rushed at us, while we stopped. He came to within about 10 mtrs. then stopped with his forefeet, raising a small cloud of dust. The cow now started to flee, and the bull turned and followed her.

Obs. Nr. 42: When driving from the Galana River in the direction of our main observation hill, we saw a subadult bull moving in our direction from the right. We stopped and sat on the bonnet of the car with the cameras ready. When 15 mtrs. away he noticed the car and approached, showing slight suspicion. After having faced us while walking hesitantly for a few seconds, he nevertheless crossed the track 6 mtrs. in front of us. But now he was suddenly reached by our scent, snorted, rushed forward with his head lowered and fled, maintaining the general direction he had been following before.

Concluding remarks

It is only some decades or – in other regions – some years, since rhinos have encountered cars. Regional, individual and momentary variations in the reactions of rhinos to cars are remarkable. Most striking in many cases are these:

- indifference to cars if they do not approach too rapidly and too noisily;
- reactions to cars as gratifying objects for chasing;
- inquisitiveness and exploratory reactions by which the rhino "is feeling out" the situation or the properties of the car.

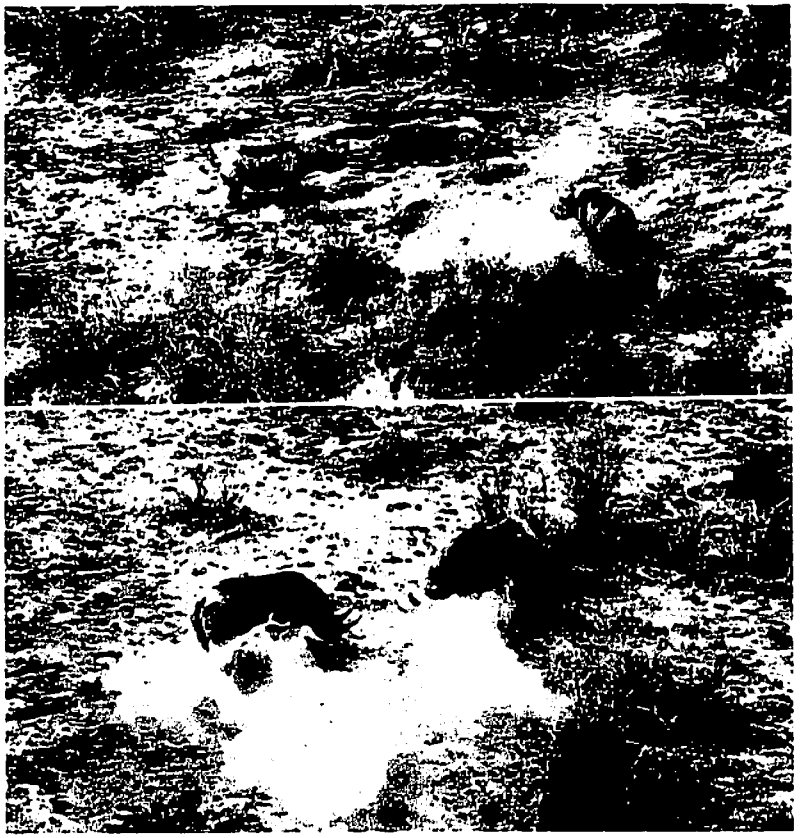

Figure 22. Defensive rush of a mother against a bull, caused by a low flying aircraft.

3. Reactions to low flying aircraft

During our flights over the study area we observed the following possible reactions of rhinos:

- Sometimes lying rhinos lifted the head but did not rise.
- Others rose, but did not move.
- Most rhinos however, fled with tail up. When the aircraft (helicopter) followed a fleeing rhino closely, it normally galloped with head and tail low and tried to find cover in bush.
- When a bull was with a mother and calf, the bull normally had a flight route of his own. On several occasions bull and cow, coming from different sides, approached one another during their flight. Then a defensive rush *(Fig. 22)* of the cow could be observed, which the bull parried with lowered head.
- Some rhinos did not move, but stood in a threatening posture and turned to face the aircraft. This reaction resembled their behaviour towards elephants which we have called "holding the ground" (see: IV. A. 4.).

- In similar cases a short rush against the helicopter could occur.
- Near Malindi road some bulls were observed who came trotting towards the aircraft, clearly with the intention of attacking and chasing it. Most probably these bulls transferred to aircraft the response which they normally showed to cars in this area.

To sum up we can state that in reacting to aircraft, rhinos try either to escape and to hide, or to "hold their ground" and defend themselves on the spot, or to attack and chase the source of disturbance.

General remarks to rhino and man

The reactions of rhinos to man in his different manifestations reveal, that the rhinoceros does not recognize man himself. Therefore it is understandable that different types of stimuli caused by man elicit quite different responses.

V. Ritualized behaviour patterns of daily activity

A. Problems and aims of investigation

In higher vertebrates with their complex way of life, the need for social signals and, generally, for means of communication is obviously very high.

Particulary in animals living in organized groups, social integration is maintained by the permanent tuning-in of all members. This permanent process has to achieve a working social unit by coordinating differentiated individuals, "personalities". Social integration therefore requires a highly differentiated system of communication. Obviously many activity patterns have adopted secondary social functions through modifications in shape, which serve these functions: they have developed a more pronounced signal quality, partly by changes in their dynamic aspect, partly by conspicuous body structures. In many cases the original function has been dropped for the benefit of the communicative function.

In its most comprehensive sense ritualization denotes these modifications in shape serving communicative functions; and behaviour patterns which have lost their original function in favour of communication are called symbolized or symbolic. One might be inclined to assume that almost solitary animals such as rhinos have not much need for communicative behaviour. Yet, it is the solitary way of life for which communication within the population must be an issue of major importance. In the rhino neither their optical nor their acoustical manifestations of presence comply with the need for communication within the population; this function is accomplished by the medium of scent.

In the rhino a number of behaviour patterns which imply the production of scent traces, mainly defecation and urination, appear to be ritualized. The assumption seems justified that ritualization in this context also functions in increasing the efficiency for communication. But this general statement is far from a full description, and needs to be completed by motivational and functional analysis, and, if possible, with some insight into the character of ritualization in the behaviour complex in question. The results of our observations made both in Amboseli Game Reserve and in Tsavo National Park are outlined in the following sections.

B. Defecation

1. Normal features of defecation

As has been described more or less accurately by several observers, the black rhino does not drop its dung indiscriminately, but it maintains "lavatories". These special dung places occur very frequently along main tracks, occasionally near moving-feeding tracks, and they are widely scattered in feeding areas. Very large dung heaps are found near common watering places.

In the study area in Tsavo National Park East, where nomadism of the rhinos is far more pronounced than in Amboseli, all dung places are used by many individuals. In contrast we found one area in Amboseli, which was frequented by one rhino only, namely the earless bull "Pixie". This bull maintained "private lavatories" in this special area.

Most dung places are next to a small tree or a bush. Some are used from one side only, others from two or more sides (see Fig. 7). Difference in usage may be explained by the presence or lack of vegetation or other obstacles nearby, which determine the possibilities of access to the dung place.

The usual patterns of defecation are as follows: Facing the dung place and sometimes clearly sniffing at it; turning on the spot; lifting the tail followed by defecation, and scraping with both hindlegs alternately.[5]

Scraping results in breaking up and spreading out the fresh dung. At the same time two shallow ditches are dug into the dung and even into the soil underneath. After scraping the rhino leaves the place.

Obviously two components of these patterns of defecation imply ritualization, namely the restriction of defecation to lavatories, and scraping simultaneously with defecation proper. Before discussing the benefit of lavatories and of scraping for communication, we shall discuss the variability of defecation and those characteristics which reveal ritualization.

2. Modified defecation

The features of defecation are often modified, and in most cases these modifications are connected with special features of the social situation. In the mother-child-unit, defecation of one individual often stimulates defecation in the other. In this context the following observation made in Tsavo East with the tame orphan rhino "Rufus" is significant: D. Sheldrick could stimulate "Rufus" to defecate by scraping with his feet.

In some cases observed, normal defecation by the mother stimulated defecation in the calf with reduced ritualization components, as shown in the following observation:

Obs. Nr. 43: A mother and her calf walked along a main track towards the river. At a bifurcation of the track, the mother defecated at a lavatory. The calf stopped meanwhile, defecated onto the track and, without scraping, left the place and followed its mother.

[5] Several authors have observed that before defecating rhinos, especially males, "sweep" the dung pile with the upper lip and the base of the anterior horn. *Goddard* (1967) furthermore stated that the animal may shuffle through the dung pile keeping the front and hind legs rigid, and that after defecation small thorn trees near the pile are sometimes demolished. In the Tsavo population, sweeping movements with the head, smashing of a shrub, and walking with stiff legs were observed only in the context of the complex bull ceremony and not of defecation.

In this case, the example of the mother induced the calf to follow suit, but the situation did not elicit the components of local fixation and scraping. In other, similar cases local fixation was missing, but scraping occurred to a reduced degree. The "transfer" of defecation was also observed in a few cases between bull and cow. The following observation illustrates this fact and at the same time shows ritualization in a reduced form in a special situation.

Obs. Nr. 44: While we walked up a little valley, a bull and a cow further up the valley were alarmed by our scent. They ran up one of the soft slopes, and at the top, where they were no longer reached by our scent, they stopped and defecated almost simultaneously 2 to 3 mtrs. from each other. The cow did not scrape at all, the bull only very cursorily.

As shown in observation Nr. 16, disturbance by man does not necessarily reduce scraping. In several encounters with male rhinos, who were not alarmed by human scent, but by oxpeckers or by the noise of a car engine, defecation was combined with intense, even exaggerated scraping.

These different examples suggest that defecation itself, its restriction to a lavatory, and its combination with scraping, are closely related to special circumstances of the actual situation. The most striking fact is the occurrence of defecation and of intense scraping in encounters with man and car. But here we have to add the fact that encounters between rhinos have the same result.

As will be discussed later, scraping on its own is a normal reaction when bulls are "showing off" and ready to face a rival. A special bull display in which scraping plays an important part, will be discussed later (V.D. Complex bull ceremony). Finally defecation with vigorous scraping occurs in yet another situation, that is when a bull comes upon a car track which has been used recently. The resulting portion of dung at the border and scraping traces across the whole track were often noticed.

3. Motivational and functional aspects of ritualized defecation

The facts mentioned above give access to the motivation of ritualized defecation in the rhino. Defecation can be stimulated by an intimate partner, mainly the mother, who sets the example. Again excitement aroused by an encounter can result in defecation. If the emotion has a quality of aggression or imposing, scraping is emphasized.

In rhinos an encounter is not restricted to optical or visual stimuli; olfactory stimulation is also important, especially in revealing the presence of another member of the species. Now the presence of scent is not necessarily linked to the presence of the individual who produced it. Scent traces might substitute the producer. In fact a car track can release the same type of defecation with vigorous scraping as does an actual encounter.

Scent traces, accordingly, act as "substitutes" and bring about "indirect encounters" or "indirect communication" within the population. This leads to the functional aspect.

Scent traces can serve the purpose of communication. Communication will benefit from an evolution which tends to make production and distribution of scent traces less incidental.

In fact one result of ritualization is the existence of discrete, localised lavatories, which justify the term "scent-marks" (SCHENKEL 1966). Undoubtedly an organised scent-marking system is more efficient as a system of olfactory communication than incidental traces set by random defecation.

The function of scraping combined with normal defecation has yet to be defined. Scraping in fresh dung also leaves localized scent traces, not at the dung place, but on the track of each individual. When the rhino rubs its hindfeet in its own fresh dung, the soles are covered with smelly substances which will impregnate each footprint while the rhino is moving.[6] In fact, observations have revealed many times that rhinos are perfectly able to follow the scent track of another individual, even on a track system which has been used by several rhinos not long before.

There is yet another aspect of ritualized defecation to be discussed; the maintaining of private lavatories as in the case of "Pixie". In this case it is neither an intimate partner nor confrontation with another rhino or its scent traces which act as releasers. It seems that in the special case of "Pixie", defecation is almost automatized and no longer governed by aroused emotion, or it is governed by another motivation which we have so far neglected. In fact, in many scent-marking mammals and especially in territorial species, the own marks are renewed again and again. It is not difficult to understand the functional value of such scent-marking. It provides a system of potential stimuli in space which contribute to imprint familiar areas, and to regulate the activity in its relation to space generally.

Figure 23. Non-ritualized urination by a young bull.

C. Urination

1. Non-ritualized urination

In bulls and cows urination occurs with and without ritualization. When urinating in non-ritualized manner, the bull stands motionless and releases a continuous, slightly pulsating stream of urine downwards and backwards (Fig. 23) onto the soil, where a ring of white foam may form. This type of urination was not often observed in adult bulls, while non-ritualized urination is the normal type seen in cows. The cow releases urine in a continuous almost vertical stream without pressure, which is interrupted and pulsating towards the end of the process.

2. Normal features of ritualized urination

When urinating in ritualized manner, the bull ejects one to four bursts of urine horizontally backwards (Fig. 24). Obviously because of pressure, these bursts take the form of a horizontal shower of very fine droplets, which may reach as far as 3 to 4 mtrs. away. The shower is usually aimed at a bush or shrub; in open grassland, however, the urine need not be squirted at a special object.

[6] This has been confirmed by GODDARD (1967, E.A. Wildlife J. 5: 133–150).

Figure 24. Ritualized urination by a fullgrown bull.

We never observed a bull sniffing first precisely at the spot to which he then squirted urine, but it could well be that he had nevertheless perceived its scent qualities when its head had passed nearby.

In cows, ritualized urination consists of one single squirt; a small quantity of urine is ejected with little pressure. The squirt is not aimed at a special object. When the cow is moving, she may stop for some seconds, squirt, and immediately walk again.

3. Motivational and functional aspects of ritualized urination in bulls

Bulls were observed to urinate in ritualized manner in the following situations:
- when walking slowly and feeding occasionally,
- on more or less circular trips during which they seem to investigate their surroundings, in following scent tracks, and in waiting on main tracks,
- in the context of an encounter with another bull,
- when stimulated acoustically by engine noise or by man on foot, especially when "called",
- in the context of a "complex bull ceremony", which will be described later (V. D.).

Ritualized urination in encounters deserves special attention, because it reveals the underlying emotion or excitement. The following observations illustrate such encounters:

Obs. Nr. 45: One morning early, a bull was feeding occasionally while moving slowly and without definite direction. Another bull, coming from the river and walking speedily in the direction of the Yatta Plateau happened to come across the feeding bull. The latter was more or less downwind and therefore the first to react. He remained on the spot, facing in the direction from which the other bull was to come. When this one was within 7 mtrs. of the waiting bull, he also became aware of the other and stopped. For more than half a minute both bulls stood motionless. Then the one who had been feeding in the area, slowly turned to the left, first apparently stiff-legged, then more and more relaxed. Simultaneously the other also moved, first with some tense and hesitating steps, then showing decreasing tension. Eventually he took up his former gait and direction, while the remaining bull squirted urine onto a bush.

Obs. Nr. 46: One evening a bull had followed closely a cow with subadult son towards the watering place. Another bull stood there on an open flat place. While cow and son went to water, their companion faced and threatened the other bull. This one however stood his ground. Eventually, after having rushed at each other screaming, the bulls separated. The newcomer went towards the water, and when passing the *Suaeda* bush girdle on the river bank, scraped vigorously and squirted urine onto a bush. The other bull approached a bush near the place of the encounter and also squirted urine.

In both cases (Nr. 45 and 46) urination occured while tension was decreasing. This is not a necessary condition. In encounters between rhino and man or car, squirting of urine sometimes occurred also during the introductory phase.

In bulls, ritualized urination is more or less congruous to ritualized defecation, whereas in cows it is much more restricted in its function.

It is most likely that ritualized urination in cows is connected with a special phase in the oestrous cycle. This does not exclude the possibility that it is the expression of excitement aroused by an encounter. On the contrary, the special status in question seems to imply a special type of excitability. Since ritualized urination in cows is not a daily activity, it will be discussed later in the context of mating (VII. A. and B. 3.).

D. Complex bull ceremony

Bulls were often observed to perform a complicated ceremony when they were alone. The same ceremony occurs, often at higher intensity and repeatedly, in certain cases of association of a bull with one or several cows. The whole performance contains the following behaviour elements:
- sniffing at a shrub or a low-growing isolated bush,
- an outburst of aggressive snorting in attack posture with or without a short and quick step forward,
- intense sideways rubbing of the nose-mouth region on the shrub or bush,
- horn-beating sideways with intensified sideways movement of the head which results in smashing the plant completely,
- stepping forward over the plant with dragging hindfeet,
- pouring bursts of urine over the plant,
- stepping backwards whereby each hindleg performs steps such as scraping kicks backwards,
- repetition of stepping forward and backward in the manner described.

It must be mentioned that the whole performance is not entirely a stereotyped sequence. The order of succession may change and sometimes one or the other element is dropped. The ceremony has in common with ritualized defecation and urination that it occurs as a kind of display in a special social situation and also as a performance of the bull on his own. In both cases we have to expect that it has an appropriate function.

As a social display it was observed only in bulls associated with one or several cows, but even in the case of such association it was seen only occasionally. The following observation illustrates this special situation.

Obs. Nr. 47: One evening, the heavy longhorned bull, often seen in the area of Observation Hill in Amboseli, was with three cows, the two females mentioned already which are most probably mother and daughter, and the younger and slightly smaller cow also often seen in the same area. The young cow showed special interest in the bull and a special kind of excitement in his presence. While they were feeding in shrub under high trees, he squirted urine whereupon she approached him repeatedly and then suddenly ran off for perhaps 20 mtrs. with tail up, as in flight. During these phases of excitement she several times squirted a small quantity of urine. The bull responded by walking away to an open place covered with dense grass and scattered bush and shrub. At a distance of approx. 30 mtrs. from the cows he repeatedly performed the ceremony described above, each time changing the place of performance. The three cows moved slowly towards the bull, but the small one was obviously most impressed. She again approached the bull and then performed an excited pseudo-flight.

On several other occasions when the same four rhinos, or only the bull and two of the cows were observed together, the bull did not show the display, but neither did any of the cows squirt urine in a ritualized manner. Apparently the small cow was at the beginning of heat, in a phase of "prudity" and the bull was stimulated to display by her status and responsiveness. Yet, premating contact shows many other variations, some of which will be described later (VII. B.). In Tsavo National Park East many encounters or associations between bull and cow were observed, but only seldom did a bull perform parts of the ceremony in such a situation.

The complex bull display has the character of "showing off" with elements of symbolized aggression. The latter are not addressed to the female, but to a plant which seems to serve as a substitute for a rival. Similar aggressive display occurs in the courtship of many vertebrates, the most famous case being the "Triumphgeschrei" of the gander (HEINROTH 1910, LORENZ 1963, FISCHER 1965). However, the problem remaining is the fact that the ceremony occurs also when a bull is alone. Several times we observed bulls performing the ceremony near a main track, and smashed shrubs near tracks, with scraping and dragging traces nearby, reveal that this must happen frequently. We also observed a bull performing the ceremony in a feeding field with a wallow nearby, obviously a place where rhinos remained often. It is quite likely that scent traces of other rhinos act as releasers of the display. But what is its function? Undoubtedly, rubbing, hornbeating, trampling, urinating, and scraping produce a whole set of scent marks which are, over a limited period of time, manifestations of presence of a bull (SCHENKEL 1966).

E. Scraping

Scraping has been described above as part of ritualized defecation which can occur when a rhino is associated with another one, when it encounters another one or man, and also when it is alone. Scraping is also part of the complex bull ceremony which occurs in the presence or absence of cows. Finally it is released in encounters as a gesture on its own. In the latter case it appears as a displacement activity revealing inhibited aggression.

If occurring as a ritual element of defecation or of the complex bull ceremony, scraping has lost its independant motivation. Yet it still seems to express a component of aggressiveness or showing off. But if the actor is on its own, there is no receptor to respond to the gesture of scraping. Clearly as part of the rituals of defecation and the bull ceremony, scraping has a "new" function: it impregnates the track with individual smelly substances.

We may conclude that scraping as an element of ritualization has its origin in the direct encounter where it still occurs. By its integration into ritualized ceremonies it has lost its independant motivation and contributes to a new function.

F. The scent-marking system: concluding remarks

The rhino disposes of a complex system of olfactory communication within the population. Ritualized defecation occurs in both sexes. Its restriction to lavatories produces a system of scent marks, its combination with scraping results in individual scent tracks. Bulls dispose of two more scent-mark systems, firstly by ritualized urination, secondly by the complex bull ceremony which produces complex scent-mark sets. Female rhinos have no similar system of their own. Their poorly ritualized urination has its function only in the context of mating. The more pronounced manifestation of presence (or epideictic display, according to WYNNE-EDWARDS 1963) in males than in females is also found in other mammals and in vertebrates generally, be it in the sphere of optical, acoustical or olfactory communication.

In the rhino the behaviour patterns by which scent marks are produced occur also in encounters. There, they are clearly connected with special characteristics of the situation and correspondingly with a special emotion. The importance of olfactory stimulation in the rhino may help to explain why "indirect communication" has been developed with scent traces as substitutes for other members of the species. The efficiency of such a communication system will increase with appropriate ritualization; a scent-marking system proper is the result of such ritualization.

The scent-marking system of the rhino does not only imply the manifestation of presence of each individual according to its sex, and act as a system of communication bringing about the continuity of the population, but also contributes to shape the environment into a living area which provides appropriate stimuli for the regulation of daily activity in space.

VI. Behaviour in direct contact between rhinos

A. Avoiding and provoking encounters

Rhinos were frequently observed to notice one another, but apparently without any intention of meeting. In some cases they could hear one another easily while feeding, but paid no attention. On other occasions, one individual was feeding and the other walking quite nearby, or they were walking in different directions. In such situations rhinos listened perhaps in the direction of the other animal, but they passed one another without making closer contact.

In the evening, when rhinos moved along a main track to water, it often happened that one rhino, walking quickly, approached another downwind, who was moving slowly, or feeding near the track, or lying on a wallow nearby. When about 30 mtrs. from the other, the approaching rhino changed from the main track to a parallel secondary track and overtook it. The other animal might face the first for a while with ears erect, but then would continue with its activity.

But, obviously, rhinos do not always avoid one another. In a number of situations they usually want to make contact; either both of them, or one of the animals concerned makes an appropriate effort and the other gives way to it:

- Mothers with calves when coming near one another accidentally, often approach for a brief meeting. This was most frequently observed in the mornings.
- Rhinos frequently come together at wallows. Usually it is the wallow which attracts them, not the opportunity for social contact. Sometimes weak competition arises over the privilege of using the wallow.
- Bulls make contact with cows in the feeding areas, on main tracks, and at watering places. Cows may reject the bull, may show "prudity" or tolerate the bull's presence.
- As has been pointed out previously, the watering place is quite generally a meeting place. Bulls often remain there for hours, and all kinds of encounters occur.

In the following sections we describe behaviour patterns of rhinos in encounters among themselves.

B. Encounters between females and/or mother-child-units

When mother-calf-units meet in a feeding area or on a wallow, the encounter is peaceful, and normally a special "greeting" ceremony takes place, as is shown in the following observations:

Obs. Nr. 48: A mother with a $^3/_4$ grown calf and one with a $^1/_2$ grown calf moved slowly across a soft slope in approximately opposite directions. When their paths had almost crossed at a lateral distance of perhaps 30 mtrs., both groups changed their direction in order to meet. The mothers were in front, each with her ears focused on the other group, while their calves were behind. When at a distance of 3 to 4 mtrs. of each other, the mothers stopped for about 20 seconds. During this time they obviously relaxed. They then approached and touched one another with the nose, presumably sniffing each others's scent. Meanwhile the calves came from behind their mothers and also greeted one another. Then the older calf touched noses with the mother of the smaller one; but when the other mother approached the smaller calf, it avoided contact. Apparently it lacked self-confidence. The four rhinos remained together for some further seconds, then separated and went in different directions, the mothers leaving first, the calves remaining together for some seconds, then following their mothers.

Obs. Nr. 49: A mother and her subadult son were lying in a wallow, when a heavy cow accompanied by a younger cow, presumably her daughter, and a subadult bull, her son, approached slowly. When the latter were about 30 mtrs. away from the wallow, mother and son rose with ears focused on them, and the approaching animals also had their ears focused in the direction of the wallow. When 20 mtrs. away the newcomers changed direction slightly and went under a small tree 10 mtrs. from the wallow. There the two cows remained for several minutes, while the subadult son walked to the wallow, where greeting took place. This was brief between the cow and the newcomer, but prolonged between the two subadult bulls, where it developed into a kind of symbolic butting, with one withdrawing, the other following up with interchanging rôles. Then all three stood on the wallow. Now the two cows which had meanwhile remained under the small tree, came to the wallow as well. Again greeting occurred. After standing for several minutes on the wallow, the bull belonging to the two females lay down, and within approximately 3 minutes all five rhinos had settled down. Later, the cow and subadult bull which had been on the wallow earlier, were the first to leave and to start feeding.

In most cases in which rhinos on a wallow were approached by another, they rose and faced in the direction of the newcomer with ears erect. The newcomer never came immediately to the wallow, but stopped before or near the edge. Then some kind of reciprocal "measuring" took place, in which self-assurance of the individuals involved, urgency of the need to wallow in the newcomer, and possessiveness or intolerance of the resident were the varying factors. The following observations show some variations of the resulting scene:

Obs. Nr. 50: A cow A lying on a wallow was approached by another, B, and rose. The newcomer B approached hesitantly and stood near the wallow for perhaps half a minute without facing the resident. A lay down again. When the newcomer B lowered her head to sniff the soil – a preparation for lying down – A jerked her head up performing symbolized horning, whereupon B lifted her head into normal position. After some time she moved her head down again, but A again responded with empty hornpush. The sequence was repeated several times. Then the cow B turned off and started to feed in a "lukewarm" manner near the wallow.

Several times she tried again to enter the wallow but she did not dare to do so because of the other cow. Eventually she lay down just outside the wallow.

Obs. Nr. 51: A mother C and her subadult son had been lying on a wallow. Mother C rose and fed nearby then stood "waiting" for a while. Mother D with a halfgrown calf approached the wallow. The subadult bull rose. When mother D stepped onto the wallow, he backed two steps and approached his mother. Mother D walked into the centre of the wallow followed by her calf and stopped there. The calf lay down and suckled for about 4 minutes, whereupon mother D and calf left. After they had gone, the young bull continued his rest.

In some few cases, after standing near one another for some time, the newcomer instead of the resident lay down first, and the resident followed suit.

On large wallows up to four rhinos were seen to arrive one after the other, and at each new arrival all the residents rose and then lay down again. In all these cases, rhinos which did not belong together did not lie in close contact, but with at least 2 mtrs. between them. When three to four rhinos visited the same wallow, it could happen that an individual could not find a place on the soft soil at the required distance from the others. Then it would often lie down outside of the wallow proper.

C. Non-mating contact between bull and cow or mother with calf

On wallows similar scenes were observed between bull and cow as between cows. On the following occasion a bull actually defended a small wallow against a mother with calf.

Obs. Nr. 52: A bull was lying on a small wallow. When a cow with half-grown calf approached, the bull rose and waited. The cow came very close, facing the wallow. When her head was within two mtrs. from that of the bull, he stepped back two steps and then rushed forward about the same distance with his head lowered, stopping himself suddenly with his forefeet, and raising a small cloud of dust. The performance was identical with "holding the ground" in encounters with elephants. As the cow still remained on the spot, the bull repeated his steps backwards and then the forward rush.

In feeding areas it is usually the bull who approaches the cow. Some different types of approach have been observed and the cow's reaction also show some variations.

The bull may approach the cow without hesitation; then she will most probably attack him while puffing rhythmically. In all cases observed, the bull turned on the spot and trotted or even galloped as far away as he was chased by the cow, that is from 5 to 300 meters. Often a bull approaches a cow very carefully without facing her or moving precisely in her direction, and so may remain near her for some hours without being molested. On the contrary, a weak bond may develop between the two animals as evidenced by the correlation of their activity, e.g. feeding, resting, moving towards water etc. Sooner or later such an association dissolves without complication or without special ceremony.

The intensity of the bond developing between bull and cow shows variations. In the more static rhino population of Amboseli Game Reserve, those bulls and cows who live almost permanently in the same area, most probably know each other individually, and they soon become quite intimate when they meet. They may for instance sleep in close contact. On the other hand this was only rarely seen in Tsavo National Park East. A nose to nose touching between bull and cow, similar to greeting in cows, was observed a few times in Amboseli, but never in Tsavo.

D. Encounters between bulls

Surprisingly often, two bulls were observed near one another i.e. at a distance of 30 to 60 mtrs., and remained so for a considerable time without actual contact. On many occasions it was obvious that one bull was downwind of the other; therefore at least one of them knew about the other's presence. It has been stated above that rhinos deliberately avoid meeting one another when moving towards water. The following observation shows the same fact in a feeding field.

Obs. Nr. 53: A was feeding on a soft slope of a little valley. B came walking up the valley on the same slope, moving parallel to the river bed. A was downwind. While B came nearer, A slowly moved towards the river bed, feeding continuously. The paths of the bull crossed one another at a lateral distance of about 30 mtrs. but they took no further notice of one another.

Many encounters occur accidentally. Bulls then usually remain motionless at a distance of 6 to 10 mtrs. of one another, each apparently "testing" the other's intentions. Then they slowly separate again as shown in Obs. Nr. 45. On a few occasions, one bull was apparently following the scent trail of a cow, when he heard another animal perhaps 30 mtrs. away. He walked or even trotted in its direction. When he was within 10 to 15 mtrs. of the other who happened also to be a bull now facing in his direction, he stopped and immediately ran off. As has been mentioned (Ecology, II. C. 2.), the same reaction was observed in a bull who had approached ostriches. It might be interpreted as caused by a situation completely different from that which the bull had expected.

Often bulls prepared to encounter other rhinos were observed near common watering places and near main tracks. Here reciprocal "testing" of bulls with imposing and threatening behaviour was seen on several occasions. The following two observations show the behaviour patterns which most often occur in these situations.

Obs. Nr. 54: In the encounter (Obs. Nr. 46) between bull A who had accompanied a mother with a subadult son and B who had been standing in the flat open space, the bulls faced one another with heads slightly lifted, in imposing posture. A then approached B with very slow, short, stiff-legged steps. His nose was pointing forward almost horizontally. B faced him, but did not move. When A was 6 mtrs. away from B, he turned to the right and with stiff steps slowly circled around B, who turned on the spot, always facing A. After having walked a semicircle around B, A faced B again and approached him with stiff legs and nose horizontal. B first waited, then rushed forward with lowered head (Fig. 25). A also lowered his head. Both bulls screamed and puffed, then stopped nose to nose, with their first horns almost touching each other. After both had screamed in repeated outbursts, A backed and once more circled around B for some steps. He then walked off in direction of the water. As already mentioned, when 25 mtrs. away, A scraped and squirted urine onto a *Suaeda* bush, and B moved some steps in the opposite direction and also marked a bush with urine.

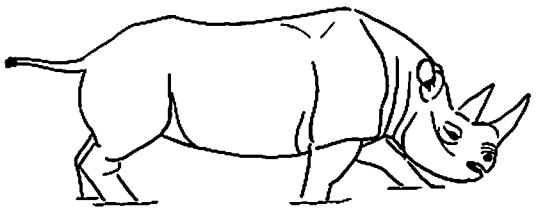

Figure 25. A bull rushes against his opponent, screaming and with his head lowered.

Obs. Nr. 55: At about 4.30 in the afternoon a bull, C, waited near the most frequented track to water in area A. Another bull, D, came moving along the track to water. When about 15 mtrs. from C, D slowed down, adopting a not very pronounced imposing posture. C stepped backwards off the track for 4 to 5 mtrs. scraping vigorously with his hindfeet, while D advanced slowly. Now C also advanced with nose stretched forward horizontally, whereupon D stopped in imposing posture. Again C backed, scraping with his hindfeet and D advanced stiff-leggedly. When about 6 to 8 mtrs. apart, the bulls rushed at one another and stopped with stiff forelegs, raising clouds of dust. They now faced each other with lowered heads, their first horns nearly touching. They undoubtedly screamed, but the observer was too far away to hear it. After having remained in this position for more than half a minute, D backed very slowly; but when C now stepped forward with lowered head, D did so too, and once more dust rose and the bulls threatened each other with horns almost touching. After another phase of immobility, D again backed very carefully, and this time C did not advance. When the distance between them was about 5 mtrs., both slowly turned. D continued his trip along the track, while C once more scraped vigorously and then followed D at the same very slow gait. After walking for about 50 mtrs. – keeping a distance of 15 mtrs. between them – D stopped and turned on the spot, displaying laterally in imposing posture. After some more steps C also stopped, and both bulls remained stationary for about half a minute. Then D turned again slowly and continued his trip, while C left the track and walked slowly into the adjacent bush.

Obs. Nr. 56: Bull E lay on a wallow. When bull F approached, he rose. F now advanced slowly in imposing posture and had almost reached the edge of the wallow, when E backed two steps and then rushed forward ("holding the ground" display). F immediately did the same and both bulls stopped just in front of each other rising a cloud of dust. After remaining in this position, horn to horn, for almost half a minute both backed one step, then they rushed again at each other. This was repeated several times more. After some 3 minutes of reciprocal threatening, E withdrew slowly and F had become "owner" of the wallow. He waited until E was approximately 20 mtrs. away, then he lay down.

The main behaviourial elements occurring in the context of these encounters are:

Forms of showing-off with weak components of aggressiveness:
- stepping backwards with scraping
- imposing posture, frontally or laterally displayed

Forms of imposing with a marked component of threat:
- stepping forward stiff-leggedly in imposing posture
- circling around the opponent in the same manner

Forms of threat proper:
- stepping forward with nose stretched forward horizontally
- rush with sudden stop in front of one another with lowered head and with screaming
- remaining in front of one another with lowered head and first horns almost touching, sometimes screaming in the beginning

Twice one bull was observed chasing another at full gallop. On one of these occasions, we saw just the beginning of the chase which was accompanied by repeated short snorts. In neither of these cases did we witness the beginning of the whole encounter. As has been stated already (Ecology IV) one of these chases ended when the pursuer gave up. In the other the pursuer reached the pursued and, with his first horn, jabbed him in the rump. The pursued tried to avoid being jabbed and changed direction in quick sequence. When he fell, the other stopped next to him with lowered head, then walked away. The defeated bull rose and walked away in the opposite direction.

It should be emphasized that really serious encounters among male rhinos are extremely rare, and even threatening or chasing are not at all frequent. Yet, bulls do not appear as relaxed as cows, and especially mothers, when they meet. They usually try to avoid meeting and in most cases when they meet accidentally, they separate as soon as they realize that the other has no intention of attacking.

Finally it should be mentioned that most reactions of rhinos to other larger animals and man are basically those observed among rhinos themselves; the only exception is the strong or even extreme component of fear in some of the encounters with man, and especially in the reaction to human scent, in regions where rhinos have been persecuted by man.

VII. Mating behaviour

A. Period of increased sexual activity in a population and isolated mating

As has been stated (Ecology V. C. 4.) a high percentage of babies was observed in July/August 1965. This means that a larger part of the cows had come on heat almost simultaneously in March/April 1964. During this short period sexual activity must have been exceptionally high. Another period of this kind was observed at the end of July 1964. Overnight, sexually motivated activity started in the area, involving a number of bulls and cows. On several occasions cows were seen to urinate in the ritualized manner described above (V. C. 2.). Bulls often followed scent tracks with the nose almost on the ground. Sometimes a bull was apparently unable to find out where the cow had gone. He followed a track continuously, then stopped and turned to the left and right sniffing carefully. Sometimes he then followed the scent track on which he had come, in the opposite direction, and again turned to the left or right, testing the adjacent terrain carefully. Occasionally a tracking bull might stop and sniff for a long time within a small area, eventually restricting this investigation to one spot. Here he sniffed for 10 to 20 seconds, at the same time moving his lips so that they rubbed against one another. He then lifted his head with the nose high and performed "Flehmen" (see IV. B. 1. a.) for about 10 seconds. Then sniffing was repeated and again "Flehmen" followed. In most cases the sequence was performed 5 to 7 times. On some of these occasions, we could state that a bull who followed the track of a cow performed these actions on the very spot on which the cow had urinated in ritualized manner. A few single cows and several mothers with half grown calves were each patiently followed by a bull. One barely adult cow approached a bull repeatedly and showed "prudity". A mutual premating bond had developed between five pairs in the area, and mating was observed once during the period.

Undoubtedly mating can also occur in one pair of rhinos on its own, without manifestation of sexual activity in other individuals of the area. This was e. g. the situation with one incidence of mating in October 1964, one in October 1966 and with one pair in close premating contact in July 1965.

B. Behaviour patterns during the premating period

Recently GODDARD (1966) has described mating in the black rhinoceros in the Ngorongoro Crater and Olduvai Gorge. As his observations are not in agreement with ours in every respect, it seems justified to give a short description of the main phases of premating as observed in Tsavo National Park East.

1. Cautious approach by the bull

When it is the bull who tries first to make contact, he follows the cow wherever she goes at a distance of 10 to 20 meters. When she stops, he approaches very carefully, avoiding facing her or walking exactly in her direction. Sometimes, when he is quite near, she steps slowly forward in intimated threat; then he turns away so as not to elicit her attack. Sometimes, however, she will really rush at him snorting. Then he will remain still, facing her, or, more frequently, will trot or even gallop off. Only when she has stopped and turned will he follow her again, perhaps more carefully than before.

2. Approach by the cow and "prudity" behaviour

As has been mentioned above, we observed a small cow repeatedly approaching a heavy bull. She faced him, came slowly closer, and when he advanced one step, most probably with the intention of performing a nose to nose contact, she snorted and ran off. The bull did not really follow her, but walked slowly in her approximate direction, feeding occasionally in between. The cow soon came back again and repeated her approach, snort and flight. Once, when the bull tried to approach her, she rushed at him, snorting violently. He remained facing her, but without showing signs of aggressiveness. She again ran away and he followed slowly in her direction.

3. Premating bond established

A premating bond develops between bull and cow. They remain together in their daily activity, especially in feeding and resting; they may sleep in close contact touching one another, and the bull may even rest his head on the cow's rump. There is no longer any hostile tension between them, and in the case of disturbance by man the bull may defend the cow. As has been mentioned already, in Amboseli bull and cow have also been seen in close contact outside the premating phase.

Sexually motivated activities during the premating period are:

- the cow urinates in ritualized manner, the bull sniffs at the cow's urine and shows "Flehmen";
- the bull approaches the cow from behind and rests his head on her rump. This is the first indication of mating intent. The second is mounting without erection, whereby the pelvic region of the bull is not as near to the cow's rump as in mating itself.

4. Mating

During mating, which lasts from 20 to 40 minutes, the male shows a sequence of behaviour patterns not mentioned by GODDARD which are repeated rhythmically over a period varying from forty seconds to a minute: he adjusts his forelegs on the shoulders of the cow, adopts an upright posture, and lifts his tail to an almost horizontal position; this position is maintained for some seconds. Then the bull's forefeet slide down somewhat laterally, while he leans over the rump of the cow, whith his tail lowered. After several seconds the rhythm starts again with the adjustment of the forelegs. Most probably this rhythm is correlated with the sequence of ejaculations. During the second half of the copulation the cow was seen to walk some steps forward or to turn on the spot; the bull is able to follow the movement without dismounting. After mating, bull and cow were observed to feed near each other and later to rest together. But on other occasions disturbance by man or by other rhinos caused disruption of the mating bond as will be shown in *5.*

5. *Interference with the copulating pair*

The majority of the cows which we have observed in premating or mating contact were accompanied by their half-grown calf. The mother-child-relation appeared undisturbed by mating, and there was no sign of tension or even conflict between bull and calf.

During premating and mating, pairs seem to have a tendency to isolate themselves. Several times we found a pair alone together in premating contact. Yet mating itself was observed in places which exert a certain attraction on a plurality of rhinos, as e.g. a wallow or a resting place next to a tree, where encounters with other rhinos are likely to occur. Self-confident bull are not easily disturbed when mating; weaker bulls also have a chance to mate, but are more susceptible to disturbance. The following observations show these different possibilities.

Obs. Nr. 57: One evening at about 17.30 on a wallow a heavy bull was mating with a mother accompanied by her calf. Another mother with calf came along a track to the wallow, and without causing any disturbance, both newcomers wallowed on one side of the large wallow while the mating pair stood on the other side. After wallowing, mother and calf continued their trip, while mating continued.

Obs. Nr. 58: A comparatively small bull was mating with a cow accompanied by a calf. After several minutes of observation when the cow began to take some steps and the bull was no longer showing the typical mating rhythm, another mother with calf approached, coming rapidly from behind a group of bushes. The bull immediately dismounted and ran about 30 mtrs. away. Greeting was performed between the mother-child groups. They then started to move, each group in its own direction. Meanwhile the bull had returned. He first took part in the slow movement of the cow with whom he had been mating, then kept nearer to the other mother, and eventually he followed a direction between both groups and soon lost contact.

The approach by the other cow caused the bull to dismount and flee, probably because as a rather weak individual he had to take account of possible interference by a stronger bull.

The flight reaction of a mating bull just mentioned, the response of bulls to "calling" as described earlier (IV. B. 1. c.), and the encounter of two bulls of which one had been following a cow (Obs. Nr. 54), together suggest that competition between bulls over a cow on heat does occur, but, that situations leading to such conflict are rather unusual.

6. *Supplementary remarks*

It has been stated by several authors, e.g. RITCHIE (1963), GUGGISBERG (1966), that mating is brought about by a very rough kind of courtship. GODDARD has already corrected this statement. He observed only some harmless jabbing by the bull. In the population of Tsavo East with its accentuated nomadism, tussles with horns between a bull and a cow must be very rare. It did not occur among the many encounters and associations between bulls and cows which we have witnessed.

GODDARD (1966) has observed bulls thrashing their heads from side to side and dragging the hindlegs in a stiff-legged gait in the context of courtship. Undoubtedly these are behaviour patterns which occur in the complex bull ceremony (see V. D.). As stated earlier, this ceremony occurred in Amboseli in a situation which was probably part of premating. In contrast, in Tsavo National Park East, we have observed the ceremony several times as a display of a bull on his own, but only once part of it, that is nose-rubbing, in contact between bull and cow. We have no explanation for these differences of populations with regard to the occurrence of male display.

GUGGISBERG illustrates mating in rhinos with a photograph showing mounting without erection. This was probably a part of premating, as GODDARD also repeatedly observed mounting in this context.

Finally it must be mentioned here, that erection can occur in bulls which are alone, especially when rising after sleeping.

VIII. The mother-child-unit

A. First period after parturition

Parturition has been observed in captive black and Indian rhinoceros (FAUST 1958, LANG 1961). We had no opportunity of observing parturition itself, or a mother immediately after parturition when eating the embryonic membranes. But we have seen mothers with very young babies. On one occasion a mother was seen still licking her newborn baby.

We lack continuous observations of the development of a baby from birth and therefore cannot correlate the following observations accurately with the age of baby rhinos.

1. *Moving and suckling*

During the first period after parturition, mother and baby move to and from water at reduced speed, especially in the very first days after birth as in the following example:

Obs. Nr. 59: A mother with a very young baby was seen moving very slowly in a northern direction after 12 o'clock in heat and sunshine. Most probably they had watered at night and were on their way back to the Plateau. The baby was of a very light grey colour, had not yet wallowed, and was not yet able to walk continuously. They moved very slowly and stopped every now and then while the mother fed on twigs near the track. The baby followed at her heels, and whenever the mother stopped, it tried to approach her nipples with its mouth, adopting suckling position which is almost at a right angle to the mother (Fig. 26). Sometimes the mother stopped a moment to cut off a twig and then walked on chewing. Her hindleg then pushed the baby's head off the nipple. But nevertheless the baby tried again to suckle at each stop. Occasionally the mother remained on the spot for a longer period, but it was impossible to find out whether the baby could really drink. At least it had not lost its interest when the mother walked again. After many efforts of the baby, the mother stood motionless for about 3 minutes for suckling. Eventually it was the baby who was obviously satisfied and gave up the suckling contact. Now the mother moved on, still slowly, but steadily and without feeding, and the baby followed closely. The mother was almost black in the saddle region and on her sides. Obviously she had not wallowed for some time.

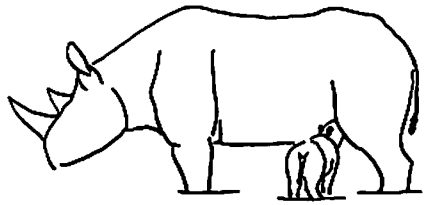

Figure 26. Suckling position of the baby.

We observed several other mothers with babies late in the morning at a distance of 6–7 kms from the river. They fed, wallowed and rested for a while, then continued their trip in a northern direction when it was already hot. But in the majority of these cases the baby did not show suckling intention continuously during the trip, and the move to the first feeding and resting area was not as slow and as late as in the above described case, which indicates that these babies were already some days older.

2. Wallowing inhibition

Mothers with very small babies are never well coated with soil and dust. They seem to abstain from wallowing, and visit wallows only to suckle and to rest. When a mother visits a wallow, the baby is next to her and as soon as she lies down, the baby follows suit. Obviously this situation results in an inhibition of the mother to wallow.

When the baby is somewhat older, the mother still wallows only on the side opposite to the baby. A mother with the baby lying on her right side was seen to wallow on her left side, then to rise and lie down on the right side of her rump. She then indeed showed initial movements of wallowing on her right side, but suddenly stopped the movement and remained lying on her brisket. In another case a mother after wallowing on one side, rose to her feet and turned on the spot through 180°, while the baby remained lying. She then wallowed her other side. Most probably the inhibition to wallow gradually weakens, but in addition the mother may learn to elude her inhibition caused by the baby next to her.

B. A few weeks after parturition

1. Feeding, wallowing, resting and suckling

When still very small and most probably only a few weeks old, babies already feed on plants. Feeding mood in the mother is usually transferred to the baby. But it seems that the baby is not influenced in its choice of food plants. Babies were seen to feed on thin single stems or twigs which did not interest the mother. The baby moves freely and quite independently, sometimes up to 25 mtrs. away from its mother. When the mother discontinues feeding and walks determinedly in a new direction, the baby will close up and then follows behind its mother.

Not only in feeding but in most other activities mother and baby appear as a unit, and generally it is the mother who has the lead function. Wallows are visited by mother and baby together. In comparison to the mother and to adult rhinos in general, the baby lies completely stretched out on one side of the body more often, and for longer periods of time, but when sleeping for a long time, it adopts the same position as an adult rhino.

Wallows are preferred places for suckling. Suckling often precedes wallowing and resting. The wallow can also be visited for suckling only.

It seems that repeated suckling intention movements as described in Obs. Nr. 59 occur only in very young babies. In the majority of suckling scenes we could not observe signals preparatory to suckling from the mother or from the baby. But it might well be that the soft bleating noise by which tame rhinos beg for food, is originally a signal of the baby asking for milk. As we were rather anxious not to disturb mothers with babies, we did not approach them too closely and may therefore have overheard such a sound.

Finally it should be added that during a short rain shower we observed a baby lying next to its mother on a wallow, and licking the rainwater which ran down its mother's side.

2. Play and exploration

Sometimes when the mother is feeding or moving slowly, the baby does not participate but indulges in locomotion plays of its own. It gallops on ahead, turns back and passes near its mother several times. The loop may lead as far as 30 or 40 mtrs. away from the mother. Occasionally the baby changes from gallop to trot and once after such play a baby came close to its mother and butted her breast, forelegs, and brisket in play.

In similar situations when the mother is feeding and moving slowly, the baby may venture around her, sniffing at plants or at the soil. The distance between mother and baby may be as much as 30 mtrs. This type of activity might be defined as playful exploration.

3. Reactions to man

It seems that very small babies do not react independently to stimulation by man. Their responses in the presence of man are elicited and formed by those of the mother. The following observations illustrate this statement:

Obs. Nr. 60: One day we drove on the Malindi track and passed near a mother with baby. When we stopped, the baby was closer to us than the mother, and it listened with its head lifted. At this moment the mother who had been some meters away, rushed forward in our direction, covered the baby in threatening posture, and then fled with tail up, the baby following at her heels, now also with its tail up.

Obs. Nr. 61: We observed a mother with a very small baby for some time. When they advanced very slowly in our direction, we withdrew and climbed the next tree. The mother fed from time to time. The baby occasionally walked in front of the mother, then waited again, and followed behind her. When they were reached by our scent, the mother first reacted by raising the tail, puffing, and then uttering the long snort while in imposing posture (see IV. B. 1. a.). The baby came close to her, now also lifting the tail, whereupon both passed near us, the mother in front, trotting with very short steps, obviously adapting her speed to her baby's capacity to run.

When the tame rhino "Rufus" was found as an abandoned baby, he was not afraid of humans. On the contrary it tried to approach them while bleating (D. SHELDRICK, D. KEARNEY, personal comm.).

This observation, as well as the local tradition in the reactions of rhinos to man, corroborate the assumption that these reactions are shaped in the baby mainly by its mother.

C. Further development of the mother-child-unit

1. Suckling

Babies suckle in standing position (Fig. 26). When grown to the size of a calf, they lie down for suckling, still oriented almost at a right angle to their mothers.

With the exception of the first days after birth where shorter suckling scenes were observed, suckling takes about four minutes each time. We do not know at which intervals the baby or the calf suckles each day, but as babies were more often seen suckling than calves, we assume that these intervals are shorter in babies. Also we do not know when and how the suckling period definitely comes to an end. No special weaning effort by the mother is needed, because suckling is impossible for the lying

calf if the mother does not stand still. The largest calf we saw suckling must have been about one year old.

2. *Lead function of the mother*

The relation between mother and offspring does not undergo conspicuous changes during the 2–3 years of its duration. In completely relaxed situations the calf also appears more independent in its movement than in tense situations as has been described for the baby. But play activity has not been observed in calves. Obviously walking, trotting and galloping are used by the calf every day as instrumental functions. When mother and calf are moving steadily, the mother usually takes the lead. Mother and calf – and even subadult – use the same wallow together. In encounters with another mother-child-unit, the mother first takes up contact as described in VI. B. She explores the actual social situation and thus protects the calf. Only after this first phase does the calf also enter into direct contact with the strangers. Especially when on or near a wallow, the mother first explores the situation, covers the calf, or competes over the wallow. This rôle of the mother was also observed in encounters with elephants.

3. *Reactions to man*

The most striking difference between baby and calf is to be found in the reaction to disturbance by man. The screeching of the tickbirds or the noise made by man, immediately elicit suspicion and alarm in the calf, whereas babies are alarmed by their mother only. The calf often appears more excited than its mother. It will lift head and tail, erect the ears, and focus them in different directions to localize the disturber, and stand at an angle to the mother, which results in the fan position typical for alarm (see Fig. 19).

When fleeing, either mother or calf may start first. But even when the mother starts first, the calf will flee in front for 50 to 100 mtrs. and the mother will cover the flight. Later the mother again takes the lead.

A bluff attack by the mother has been observed three times. Each time we were driving rather quickly on a tortuous track and suddenly and unexpectedly found ourselves in front of a mother with calf, they as surprised as we were. The mother each time performed a short rush and turned immediately afterwards and fled with the calf.

4. *Weakening and disruption of the bond between mother and calf*

As has been pointed out, mothers normally mate again when their previous calf is about $^1/_2$ to $^2/_3$ grown, that is between 1 and 2 years old. Mating does not disrupt the mother-child-bond, but when the new baby is born, the former offspring, by then $2^1/_2$ to $3^1/_4$ years old, has become independent.

The mother rejects her subadult offspring when she is near to parturition. We did not however observe this.

In a population with rather stable home ranges as in Amboseli and Ngorongoro Crater, former offsprings may later join the mother and her younger calf again. In the nomadic population of Tsavo East, on the other hand, this is unusual. In this region the permanent association between two cows of different age, or between a cow and a subadult animal was more often seen. The distance between two such partners when feeding was sometimes greater than between mother and calf; the rôles of leading and following suit were often interchanged. In a few cases each partner

wallowed independently as evidenced by different coloration. Most of these associations were probably mother-child-units which persisted because the mother had no further baby. Of the group of three animals which we often observed in Amboseli, the mother and the daughter always wallowed together, but the subadult son who often joined them, was seen to wallow simultaneously at another place.

SUMMARY: THE WAY OF LIFE OF THE BLACK RHINOCEROS

In earlier reports, interest in the black rhino appears to have been concentrated on its irritability and aggressiveness in encounters with man. In attributing an aggressive, bad, and dangerous character to the rhino, the rhino-hunter could present himself as a hero.

Since behaviour and ecology of mammals have been studied systematically, the rhino has also become the object of a more scientific approach. But until recently the aggressiveness of the black rhino has still been emphasized, deadly fights between bulls, severe fights between bull and cow and even between elephant and rhino have all been reported. In addition, attention was paid to sensory capacities, to the feeding, scent-marking and wallowing habits of the rhino. Some authors attributed territoriality to the rhino, others maintained that the rhino has a rigidly fixed daily activity program within a rather limited home range.

In the course of this systematic investigation of behaviour and ecology of the black rhino, carried out between January 1963 and October 1966, many of the above described characteristics of the black rhinoceros have appeared in a different light. Attempts were made to analyse function and motivation of a number of behaviour patterns and the ecological position of the rhino has been outlined.

As for the elephant, the only enemy of the rhino is man. Its sensory organs are not developed for detecting an enemy at a distance. They are primarily organs functioning in intraspecific communication and contact, in the selection of food, and in the orientation in the environment.

Since man has developed into a dangerous enemy of the species, the black rhino has built up special responses to man. It is not quite clear which components of these responses are innate, and which are transferred by tradition from mother to offspring. The acute smell of the rhino has become the most important sense for its protection, but it only functions when the rhino is downwind of man. The rhino has developed yet another response to the approach of man as a potential enemy; this is its reaction to the acoustical alarm signal of the oxpecker. This signal also releases an alarm response in the rhino which consists of immediate flight, or of inquisitive attention and exploratory behaviour which can lead to either quiescence, flight or attack.

The black rhino is not gregarious. Mother and child form a stable group. It is dissolved when the mother is again near parturition. Male and female associate only temporarily; usually no strong individual bond exists between them. The almost solitary way of life of the rhino requires an efficient system of communication within the population. By ritualization, the accidental production of scent traces has been developed into a scent-marking and trail-marking system.

This system brings about 'indirect' encounters, whereby the scent marks substitute for their producers. The reactions of the rhino to scent-marks including components of ritualization, appear in fact derived from responses in the direct intraspecific encounter. The scent marks represent the producers, and the reactions of the rhino to scent marks are in fact derived from responses used in "direct" encounters between animals. Undoubtedly the scent- and trail-marking system is multifunctional. It results in impregnating the whole living space of a rhino population in a very differentiated manner.

Rhinos do not live in territories. In a region in which the feeding areas extend over many kilometers away from permanent water, the rhinos live as nomads, and all the feeding areas, sleeping places, wallows, tracks, and watering places are used by many different rhinos. Impregnation with scent will give special stimulus values to all the different components of the living space, thereby facilitating orientation. It has thus a complex guiding function in the daily activity of the rhino.

The young rhino is never integrated into a herd as are the offspring of gregarious ungulates. During the period of dependence, while forming a behaviour unit with its mother, it is introduced and integrated into the living space of the population with its complicated sociological structure.

Most of the larger African mammals live in the grassland or in zones of transition between grassland and primary forest, the different types of savannah. In the grassland proper, the number of species is relatively small, concentrations of animals are temporarily high and seasonal migration of herbivores is prominent. In transitional zones large scale migration and large concentrations of animals are rare, but the number of species is relatively high. The large herbivores, by their special way of life, contribute to open the forest or at least to limit its expansion and thus maintain their own living space. The black rhino is one of the species living in the transitional habitat between grassland and forest.

In this context the elephant should be mentioned as the only mammal species that really breaks into the forest on a larger scale and opens wooded country to the vegetation and the animals of the savannah. The rhino benefits from this activity of the elephant, perhaps more so than do other species. It uses the tracks which the elephants develop. But in a savannah as in Tsavo East, elephants and bush fires succeed in converting the vegetation of a whole region from tree- und bush-savannah into open grassland. It is still an open question whether a rhino population can survive this transformation of its habitat. Under natural circumstances a new generation of elephants might migrate to another area and the bush could recover. But with the spread of human settlement and cultivation there is not much space left for the emigration of elephants. It may therefore be the task of man as a conservationist to actively maintain a certain natural equilibrium within the wildlife sanctuaries. The survival of an endangered species of the large mammals, the black rhinoceros, is at stake.

ZUSAMMENFASSUNG: DAS LEBENSBILD DES SCHWARZEN NASHORNS

In früheren Berichten wird das Schwarze Nashorn meist als reizbares, gefährliches Ungeheuer geschildert, und sogar noch in Publikationen der letzten Jahrzehnte klingt diese Note mit. In jüngerer Zeit haben die Sinnesfähigkeiten der Nashörner und manche ihrer Verhaltenseigentümlichkeiten vermehrt Beachtung gefunden. Gelegentlich wurden Beobachtungen wenig kritisch interpretiert. So wurde etwa vom Markierungs-Verhalten auf Territorialität geschlossen, oder von der Existenz gut ausgetretener Wechsel und vielfach benützter Tränken und Suhlen auf raum-zeitlich starr festgelegte Tagesabläufe mit täglichem Marsch zur Tränke.

Die vorliegende Untersuchung befaßt sich sowohl mit der ökologischen Rolle des Schwarzen Nashorns als auch mit seinen Verhaltensweisen und versucht, ein zutreffendes Lebensbild zu erarbeiten.

Keine Raubtierart gefährdet das Schwarze Nashorn in seinem Artbestand, und dementsprechend sind seine Sinnesorgane auch nicht für allseitige Sicherung auf große Distanz eingerichtet. Daher kommt die weitgehende Schutzlosigkeit der Art gegenüber menschlicher Verfolgung. Immerhin hat das Nashorn in Gegenden, wo es gejagt wird, gewisse Schutzreaktionen entwickelt. Vor allem, wenn es Witterung vom Menschen erhält, flieht es in großer Erregung. Damit ist es aber nicht gegen Annäherung unter dem Wind gesichert! Gegen diese Gefahr zeigt es eine Reaktion, welche den Gesichtssinn des Madenhackers *(Buphagus)* auswertet! Es reagiert auf dessen Alarmruf, und zwar erscheint es dabei stärker beunruhigt, als wenn es einen Menschen selbst sich bewegen oder sogar sprechen hört. Kommt es zur Störung durch den Menschen, ohne daß dessen Geruch mitspielt, so können recht verschiedene Reaktionen eintreten. Meist reagiert das Nashorn zuerst mit Aufmerksamkeit und aktivem Explorationsverhalten; als zweite Phase der Reaktion kommen Beruhigung, neugierige Kontaktaufnahme, Flucht oder – in seltenen Fällen – Angriff in Frage.

Da die Nashörner wenig gesellig leben, bedarf die Population eines leistungsfähigen internen Verbindungssystems. Ritualisation der Kot- und Harnabgabe gestalten die Geruchsspuren zu einem geordneten System der "geruchlichen Markierung". Dieses gewährleistet "indirekte" Begegnung innerhalb der Population.

Das Schwarze Nashorn lebt nicht territorial. Besonders in Gegenden, wo während des größten Teils des Jahres Wasser und Weidegebiete weit auseinanderliegen, ist seine Lebensart betont nomadisch. Es kommt nur alle paar Tage zum Wasser, und die Trinkstellen, Freßgebiete, Wälzplätze und Wechsel eines Gebietes werden von vielen verschiedenen Individuen benützt. Geruchliche Markierung stattet den ganzen Lebensraum mit einem differenzierten System von Impulsquellen aus und leistet so einen Beitrag zur zeitlichen und räumlichen Steuerung der Aktivität. Entgegen der verbreiteten Ansicht sind Intoleranz und Aggressivität beim Schwarzen Nashorn nicht besonders ausgeprägt und ernste Kämpfe selten. Sowohl hinsichtlich des Nomadismus wie auch mancher Reaktionsnormen bestehen zwischen einzelnen Populationen Unterschiede. Derartige lokale Traditionen werden in der Mutter-Kind-Gemeinschaft weitergegeben.

Das Schwarze Nashorn bewohnt den Übergangsbereich zwischen der offenen Steppe und dem eigentlichen Wald. In diesem Lebensbereich spielt der Elefant eine wichtige Rolle. Er bricht in die Grenzzone des Waldes ein, ja drängt diese zurück und

öffnet so für das Nashorn und die von ihm benötigte Vegetation den Raum. Andererseits kann ein großer Elefantenbestand zusammen mit Steppenfeuern die Baum- und Buschkomponente der Vegetation einer ganzen Landschaft weitgehend zerstören. In früheren Zeiten haben sich die Schwerpunkte der Elefantenbesiedlung vermutlich dauernd verschoben. Auf Phasen dichter lokaler Besiedlung mit beträchtlicher Reduktion der Baum- und Buschvegetation folgten Abwanderung der Elefanten und Wiederaufbau des früheren Vegetationstypus. Das ist heute nicht mehr möglich; nur noch recht begrenzte Gebiete stehen den freilebenden Elefanten zur Verfügung. Die Einengung seiner Populationen auf zu enge Lebensräume droht, tiefgreifende Veränderungen des Biotops hervorzurufen. Ihr Ausmaß und besonders auch ihre Auswirkungen auf das Schwarze Nashorn sind noch nicht vorauszusehen. Gründliche Überwachung der betreffenden Gebiete ist unerläßlich, und vielleicht ist ein Dauerzustand, bei dem auch das Schwarze Nashorn gedeiht, nicht mehr möglich ohne wohlabgewogene hegerische Eingriffe seitens des Menschen.

RÉSUMÉ: LE MODE DE VIE DU RHINOCÉROS NOIR

Ce travail traite non seulement de la niche écologique du rhinocéros noir mais également de son comportement. Aucun grand prédateur ne peut mettre le rhino en danger. De ce fait on comprend pourquoi ses organes de perception ne sont pas évolués de manière qu'il peut se couvrir dans toute les directions. C'est ici qu'il faut chercher l'origine de la vulnérabilité du rhino à l'égard de l'homme. Toutefois dans les régions où il est chassé, le rhino a développé des réactions protectrices. Lorsqu'il perçoit l'odeur de l'homme, il s'enfuit en état de grande excitation. Mais de cette façon il n'est pas protégé contre quelqu'un s'approchant sous le vent. Dans ce cas le rhino réagit au cri d'alarme des pique-boeufs *(Buphagus)* et à ce moment il est plus inquiet que lorsqu'il entend l'homme lui-même. En cas de perturbation par l'homme sans implication de l'odeur humaine, le rhino réagit de différentes manières: normalement il est d'abord attentif et exploratif; par la suite, soit il se calme, soit il essaie de prendre contact, ou bien il s'enfuit ou – rarement – il attaque.

Comme les rhinos sont peu sociaux, les individus d'une région ont besoin d'un système de liaison interne. C'est par ritualisation de la défécation et de la miction que les traces olfactives forment un système de marcage qui assure les rencontres "indirectes" entre les membres de la population.

Le rhinocéros noir ne défend pas un territoire. Dans des régions où l'eau est à grande distance des pâturages durant presque toute l'année, le rhino est un nomade. Il ne va à l'eau que tous les 3 à 6 jours et tous les abreuvoirs, les pâturages, les souilles et les passées sont fréquentés par beaucoup d'individus différents. Les marques olfactives appliquées à tout l'environnement constituent un système d'impulsions qui contribuent à diriger l'activité des rhinos.

En dépit de l'opinion générale le rhino n'est ni spécialement aggressif ni intolérant, et des duels sérieux sont rares. En ce qui concerne le nomadisme et certaines formes de comportement on observe des différences marquées entre les groupes de différentes régions. Ces traditions locales sont transmises de la mère à son petit.

Le rhino noir vit dans une zone transitoire entre la savane et la haute forêt. Dans cette région l'éléphant a un rôle écologique important. Il pénètre dans la zone marginale de la forêt, la repousse et crée ainsi un espace vital pour le rhino et pour la végétation dont celui-ci a besoin. Par contre un peuplement dense d'éléphants joint aux feux de brousse détruisent les arbres et les buissons. Autrefois les populations des éléphants transhumaient continuellement et facilitaient ainsi la régénération de la végétation. Aujourd'hui les régions à la disposition de l'éléphant sauvage sont limitées et ses migrations bloquées. Par conséquent ses populations exercent une pression permanente sur la végétation causant ainsi des changements profonds du biotope. L'effet de ces transformations sur le maintien du rhino noir ne peut être prévu. La surveillance continuelle des régions en question est indispensable et il se peut bien que le maintien d'une population équilibrée de rhinos ne sera possible que par des efforts continuels de conservation.

LITERATURE

Buechner H.K. & Dawkins H.C., 1961: Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. Ecology 42: 752–766.

Faust R., 1958: Die Geburt eines Spitzmaulnashornes *(Diceros bicornis* L.*)* in Frankfurt. Zool. Garten (N.F.) 22: 208–214.

Fischer H., 1965: Das Triumphgeschrei der Graugans *(Anser anser)*. Zs. f. Tierpsychol. 22: 247–304.

Glover P.E. & Sheldrick D., 1964: An urgent research problem on the elephant and rhino populations of the Tsavo National Park in Kenya. Bull epiz. Dis. Afr. 12: 33–38.

Goddard J., 1966: Mating and courtship of the Black Rhinoceros *(Diceros bicornis* L.*)*. E.A. Wildlife J. 4: 69–75.

Goddard J., 1967: The validity of censusing black rhinoceros populations from the air. E. Afr. Wildl. J. 5: 18–23.

Goddard J., 1967: Home range, behaviour, and recruitment rates of two black rhinoceros populations. id. 5: 133–150.

Guggisberg C.A.W., 1966: S.O.S. Rhino. Deutsch, London.

Hagenbeck D., 1966: Report on the hand-rearing of an Indian rhinoceros at Hamburg Zoo, Internat. Zoo Year Book 6: 82–87.

Hediger H., 1949: Säugetier-Territorien und ihre Markierung. Bijdr. t. d. Dierkunde 28: 172–184.

Heinroth O., 1910: Beiträge zur Biologie, namentlich zur Ethologie und Psychologie der Anatiden. Verh. d. V. Int. Ornith. Congr. Berlin 589–702.

Klingel H. & U., 1966: The Rhinoceroces of Ngorongoro Crater. Oryx 8: No. 5.

Lang E.M., 1961: Beobachtungen am Indischen Panzernashorn *(Rhinoceros unicornis)*. Zool. Garten (N.F.) 25: 369–409.

Lang E.M., 1967: personal communication.

Lorenz K., 1963: Das sogenannte Böse. Zur Naturgeschichte der Aggression. Borotha-Scholer, Wien.

Napier-Bax P. & Sheldrick D.L.W., 1963: Some preliminary observations on the food of elephant in the Tsavo Royal National Park (East) of Kenya. E.A. Wildlife J. 1: 40–51.

Parsons B.T. & Sheldrick D.L.W., 1964: Some observations on biting flies (Diptera, Mucidae, sub-fam. Stomoxydinae) associated with the Black Rhinoceros *(Diceros bicornis* L.*)* E.A. Wildlife J. 2: 78–85.

Ritchie A.J., 1963: The Black Rhinoceros *(Diceros bicornis* L.*)* E.A. Wildlife J. 1: 54–62.

Roth H.H. & Child G., 1968: Distribution and population structure of black rhinoceros *(Diceros bicornis* L.*)* in the Lake Kariba basin. Ztschr. f. Säugetierkunde. 33: 214–226.

Round H.C., 1964: A new species of *Stephanofilaria* in skin lesions from the black rhinoceros *(Diceros bicornis* L.*)* in Kenya. J. Helminthol. 38: 87–96.

Schenkel R., 1966: Zum Problem der Territorialität und des Markierens bei Säugern – am Beispiel des Schwarzen Nashorns und des Löwens. Zs. f. Tierpsychol. 23: 593–626.

Schenkel R. & Lang E.M., 1969: Das Verhalten der Nashörner. Handbuch der Zoologie VIII. 10. Teil.

Schulz K.C.A. & Kluge E.B., 1960: Dermatitis in the black rhinoceros *(Diceros bicornis)* due to filariasis. South Afr. Vet. Med. Ass. 31: 265–269.

Schneider K.M., 1930: Das Flehmen. 1. Teil. Zool. Garten (N.F.) 3: 183–198.

Spinage C.A., 1960: Some notes on the rhinoceros. Afr. Wild Life 14: 95–100.

Tremlett J.G., 1964: Observations on the pathology of lesions associated with *Stephanofilaria dinniki* Round, 1964, from the Black rhinoceros *(Diceros bicornis)*. J. Helminthol. 38: 171–174.

Wynne-Edwards V.C., 1962: Animal dispersion in relation to social behaviour. Oliver & Boyd, Edinburgh und London.

Mammalia depicta

In dieser Monographien-Serie, herausgegeben von Prof. Dr. Dr. h. c. W. Herre, Kiel, und Prof. Dr. M. Röhrs, Hannover, erschienen außer dem vorliegenden Heft:

Der Alpensteinbock *(Capra ibex* L.*)* **in seinem Lebensraum.** Ein ökologischer Vergleich. Von Dr. B. Nievergelt, Zürich. 1966. 85 Seiten mit 40 Abb. und 13 Tab. Kart. 18,— DM · **Der Blaubock** *(Hippotragus leucophaeus*, Pallas 1766). Eine Dokumentation. Von Dr. E. Mohr, Hamburg. 1967. 81 Seiten mit 53 Abb. und 5 Tab. Kart. 28,— DM · **Succession of Rodent Faunas During the Upper Pleistocene of Israel.** Morphologic, Taxonomic und Systematik der Nagetierfauna in Israel während des Jüngeren Pleistozäns. By Dr. E. Tchernov, Jerusalem. 1968. 152 pp., 130 figures and diagrams, 40 tables. Stiff paper covers 46,— DM · **Das Sozialverhalten des Rehes** *(Capreolus capreolus* L.*)* Eine Feldstudie. Von Dr. Fr. Kurt, Zürich. 1968. 102 Seiten mit 30 Abb. und 22 Tabellen. Kartoniert 28,— DM · Die Reihe wird fortgesetzt

Vergleichende Anatomie der Wirbeltiere

Von Prof. A. S. Romer, Harvard University. Aus dem Amerikan. übersetzt und bearbeitet von Prof. Dr. H. Frick, Frankfurt/M. 2., neubearb. und erweit. Auflage. 1966. 548 Seiten mit 407, z. T. farbigen Abb. Leinen 64,— DM

Der Energiehaushalt von Mensch und Haustier

"The Fire of Life". Ein Lehrbuch der Tierenergetik. Von Prof. Dr. M. Kleiber, Davis/USA. Vom Verfasser ins Deutsche übertragen unter Mitwirkung von Univ.-Doz. Dr. J. O. Gütte, Göttingen. 1967. 358 Seiten mit 78 Abbildungen und 94 Tabellen. Leinen 78,— DM

Ökologie der Tiere

Ein Lehr- und Handbuch in drei Teilen. Von Prof. Dr. F. Schwerdtfeger, Göttingen

Band I: **Autökologie.** Die Beziehungen zwischen Tier und Umwelt. 1963. 461 Seiten, 271 Abb., 50 Übersichten. Leinen 68,— DM

Band II: **Demökologie** Struktur und Dynamik tierischer Populationen. 1968. 448 Seiten mit 252 Abb. und 55 Übersichten. Leinen 84,— DM

Band III: **Synökologie.** In Vorbereitung

Die Wirbeltiere des Kamerungebirges

Unter besonderer Berücksichtigung des Faunenwechsels in den verschiedenen Höhenstufen. Von Prof. Dr. M. Eisentraut, Bonn. 1963. 353 Seiten, 52 Abb., 79 Tab. Leinen 68,— DM

Riesen und Zwerge im Tierreich

Von Prof. Dr. E. J. Slijper, Amsterdam. Aus dem Niederländischen übertragen von R. Bartels. 1967. 199 Seiten mit 106 Abbildungen im Text und auf 8 Tafeln. Leinen 24,— DM

Die Einbürgerung von Säugetieren und Vögeln in Europa

Ergebnisse und Aussichten. Von Prof. Dr. G. Niethammer, Bonn. Unter Mitarbeit von J. Niethammer und Dr. J. Szijj. 1963. 319 Seiten mit 54 Abbildungen, 26 Verbreitungskarten und 5 Tabellen. Leinen 54,— DM

Die Säugetiere Europas

Westlich des 30. Längengrades. Taschenbuch für Zoologen und Naturfreunde. Von F. H. van den Brink. 2., neubearbeit. Aufl. in Vorbereitung

Zeitschrift für Säugetierkunde

Organ der »Deutschen Gesellschaft für Säugetierkunde«. Erscheint 1969 mit dem 34. Band. Herausgegeben unter internationaler Mitwirkung zahlreicher Mitarbeiter. Schriftleitung: Dr. E. Mohr †, Hamburg, und Prof. Dr. M. Röhrs, Hannover. Erscheint zweimonatlich. 6 Hefte bilden einen Band. Jedes Heft umfaßt 4 Druckbogen (je 16 Seiten). Abonnementspreis: je Band 82,— DM, zuzügl. Versandkosten. Die Mitglieder der »Deutschen Gesellschaft für Säugetierkunde« erhalten die Zeitschrift kostenlos im Rahmen des Mitgliedsbeitrages

VERLAG PAUL PAREY · HAMBURG UND BERLIN

Zeitschrift für zoologische Systematik und Evolutionsforschung

Unter Mitwirkung zahlreicher Mitarbeiter aus dem In- und Ausland, herausgegeben von Prof. Dr. Dr. h.c. W. Herre, Kiel, Prof. Dr. Dr. h.c. Dr. h.c. C. Kosswig, Hamburg, Prof. Dr. E. Reisinger, Graz, und Dr. S. L. Tuxen, Kopenhagen. Schriftleitung: Prof. Dr. Dr. h.c. W. Herre, Kiel

Die Zeitschrift erscheint 1969 mit dem 7. Band. Erscheinungsweise: vierteljährlich. 4 Hefte von jeweils 5 Druckbogen (à 16 Seiten) bilden einen Band. Abonnementspreis je Band 98,— DM zuzügl. Versandkosten. Einzelhefte außerhalb des Abonnements 30,— DM. Das Abonnement verpflichtet zur Abnahme jeweils kompletter Bände

Lehrbuch der vergleichenden Entwicklungsgeschichte der Tiere

Von Prof. Dr. R. Siewing, Erlangen. 1969. 531 Seiten mit 1300 Abbildung. Leinen 58,— DM

Die Entwicklung zum Menschen

Evolution, Abstammung und Vererbung. Ein Abriß. Von Prof. Dr. Th. Dobzhansky. Columbia University. Aus dem Amerik. übersetzt von H. Schwanitz, Herausgegeben und bearb. von Prof. Dr. F. Schwanitz, Hamburg. 1958. 407 S. mit 215 Abb. Leinen 32,— DM

Der heutige Stand des Fetalisationsproblems

Von Prof. Dr. med. D. Starck, Frankfurt/M. Vorabdruck aus »Zeitschr. für Tierzüchtung und Züchtungsbiologie«. 1962. 27 Seiten mit 10 Abb. Kartoniert 4,80 DM

Das Gleichgewicht in der Natur

Von Dr. L. J. Milne und Dr. M. Milne. Aus dem Amerik. übersetzt von Dr. K. Meunier, Kiel. 1965. 288 Seiten. Leinen 24,— DM

Instinktlehre

Vergleichende Erforschung angeborenen Verhaltens. Von Prof. Dr. N. Tinbergen, Oxford, übersetzt von Prof. Dr. O. Koehler, Freiburg i. Br. 4. Aufl. 1966. 268 Seiten mit 130 Abbildungen. Kartoniert 28,— DM; Leinen 32,— DM

Artbegriff und Evolution

Von Prof. Dr. E. Mayr, Harvard University, Cambridge/Mass. Aus dem Engl. übertragen von Prof. Dr. G. Heberer, Göttingen, unter Mitarbeit von Prof. Dr. G. H. W. Stein, Berlin. 1967. 617 Seit., 65 Abb., 42 Tab. Lein. 78,— DM

Principia Genetica

Grunderkenntnisse und Grundbegriffe der Vererbungswissenschaft. Von Prof. Dr. A. Heilbronn † und Prof. Dr. C. Kosswig, Hamburg. 2., neubearb. Aufl. 1966. 43 Seit. Kt. 5,80 DM

Fortpflanzung und Nomenklatur im Pflanzen- und Tierreich

Von Dr. G. Luckhaus, Berlin. 1965. 83 Seiten mit 10 Abbildungen. Kartoniert 9,80 DM

Die Sinneswelt der Tiere und Menschen

Fragen, Ergebnisse u. Ausblicke d. vergleich. Sinnesphysiologie. Von Dr. I. J. Milne und Dr. M. Milne. Aus d. Amerik. von I. Schwartzkopff. 2. Aufl. 1968. 315 Seiten. Ln. 24,— DM

Tiere untereinander

Formen sozialen Verhaltens. Von Prof. Dr. N. Tinbergen, Oxford, ins Deutsche übertragen von Prof. Dr. O. Koehler, Freiburg i. Br. 2., unveränderte Aufl. 1967. 158 Seiten mit 84 Abb. im Text und auf 8 Tafeln. Kartoniert 12,80 DM

Zeitschrift für Tierpsychologie

Begründet 1937. Herausgegeben unter Mitarbeit leitender Fachgelehrter von Prof. Dr. O. Koehler, Freiburg i. Br., Prof. Dr. K. Lorenz, Seewiesen/Obb., und Dr. W. Wickler, Seewiesen/Obb. Erscheinungsweise: jährlich 1 Band zu ca. 8 Heften in zwangloser Folge, je Heft im Umfang von etwa 8 Druckbogen. Bezugspreis: je Druckbogen (16 Seiten) etwa 6,— DM. Die Hefte werden einzeln berechnet. Das Abonnement verpflichtet zur Abnahme jeweils kompletter Bände

VERLAG PAUL PAREY · HAMBURG UND BERLIN