THE BLACK RHINOCEROS (DICEROS BICORNIS L.)

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SUMMARY

The two African genera of rhinoceroses are briefly compared and an account given of the distribution of the black rhinoceros (Diceros bicornis L.). This species, which is adapted to a wide range of habitats, is now absent from or scarce in many parts of Africa where it was common only 50 or 100 years ago. It is described in detail with comments on the validity of the two subspecies D. b. bicornis and D. b. somaliensis Potocki.

Daily activity and home range of the black rhinoceros are largely related to its water requirements, and it normally drinks once in 24 hours. In order to feed it may move 5-15 miles from the watering place along regular paths; feeding takes place in the early morning and evening and the remainder of the day is spent resting in shace. A constant behaviour pattern during defaecation and urination is described.

A group or herd is usually composed of one, two or three individuals. Mating may take place at any time during the year. The disposition of individual animals is considered to be related to the degree to which they have been persecuted by man; in different areas, inhabited by hunting or pastoral tribes, a marked difference in behaviour is apparent. Instances have been recorded of black rhinoceroses being killed by elephants (Loxodonta africana Blumenbach) and by lions (Panthera leo Linnaeus).

An account is given of the structure of the horns and the way in which they are used, and of their commercial value. Poaching of the species in Kenya is carried out largely by means of poisoned arrows or leg snares.

Warning is given of the urgent need for strict measures to conserve the species. which will only survive in sanctuaries where its interests are paramount. Its decline is due not only to the impact of man but to its apparent inability to extend its range into areas where rhinos have not formerly existed. It is one of the species in most danger of extinction.

(Editorial note: this paper was written by the late A. T. A. Ritchie, Chief Game Warden of Kenva from 1923 to 1948, some time before his death in 1962. Ritchie was a fine

was the black rhinoceros, and the editorial committee consider it particularly suitable that this record of his observations should be published in the first number of the East African Wildlife Journal to which he would undoubtedly have given wholehearted support. It should be pointed out that certain facts in the paper are now outdated. Some authorities consider the white rhino to be a species of Diceros, and poaching and other effects of man's presence are now a major factor in the decline of the black rhinoceros. Even with the present degree of control poaching is rife, and if this control is materially decreased the rhinoceros will undoubtedly rapidly disappear from many areas.)

Introduction

The Rhinoceros family belongs to the order of mammals Perissodactyla; in Africa the family has two genera, Ceratotherium and Diceros.

The former, the white rhinoceros, is characterised by its larger size, a longer skull and a broad square upper lip. The latter, the black rhinoceros, has a much shorter skull and a prehensile tip to the narrow, rounded upper lip. The shape of the upper lip provides an immediate clue to the feeding habit of the two animals, the white rhino being a grazer and the black a browser. It may be noted that the terms white and black have little relation to body colour, and could perhaps more reasonably be held to apply to temperament and reputation. The white rhino is a dependable well-mannered beast, while the black is irritable and explosive, and capable of vicious and vindictive action without provocation. My knowledge of rhino is confined almost exclusively to animals in Kenya, and what I write in this paper must be read with that qualification.

DISTRIBUTION

The black rhinoceros is still fairly widely distributed over Africa, though today much less so than formerly. Its present distribution is indeed tragic when compared with a hundred or even fifty years ago, observer and naturalist whose special interest whether one considers it geographically or

numerically, for it has disappeared entirely from vast areas of Africa and in many of the parts where it still exists it is in sadly depleted numbers. Formerly it abounded in most suitable localities from the Cape to the Blue Nile and from Somaliland to the Cameroons, though it appears always to have been more plentiful on the eastern side of the Continent. Today the position, so far as I know it, is briefly as follows: in South Africa it is virtually extinct, except for a certain number in sanctuaries. Southern Rhodesia and Nyasaland have a few. Northern Rhodesia has a fair number, chiefly in the Luangwa River area. Tanganvika and Kenva are its main strongholds, and it is still numerous in some suitable areas. In Somalia, Somaliland and Ethiopia it is rare. In the Sudan there are some in the Blue Nile district with a very few as far as the Uganda border on the east side only of the White Nile. French Equatorial Africa still boasts a fair number, but only a few now remain in the north-east of Nigeria, round Lake Chad, and in the Cameroons. They have never been found in the Congo basin, but some remain in the Katanga, Rwanda and Burundi provinces of the Congo. Angola has a small number. Those animals inhabiting the area comprising northern Kenya, Somalia, Somaliland, and the Ethiopian Rift as far west as Lake Rudolf belong to the race D. b somaliensis Potocki. Elsewhere the animals are of the type race D. b. bicornis Linnaeus.

DESCRIPTION

The black rhinoceros is a large bulky animal, thick skinned and devoid of hair except for eyelashes, and ear and tail fringes. It is evenly three toed, each toe having its own hoof. It has two horns on the front of the head, one behind the other. The skin is a dark neutral grey-brown colour; the belly and under parts are lighter and more grey. There are no definite folds on the skin, except a transverse one on the foreleg above the knee and another across the nape of the neck behind the ears. The skin on the flanks is striated by narrow riblike folds which are however independent of the ribs. Measurements and weights vary greatly, but those of a large animal might be as follows from tip of nose to root of tail measured along the body curve, 12 feet 3 inches. Height at shoulder, 5 feet 6 inches. The weight of adults is usually between two and

three thousand pounds, according to Meinertzhagen (A Kenya Diary, 1957).

These data refer to the type race Diceros bicornis bicornis. A race, D. b. somaliensis, has been described from the north east corner of the Diceros range, and it is stated to be at least ten per cent smaller than bicornis. It is characterised particularly by the markedly lesser concavity of the upper profile of the skull, such concavity being two inches or less as compared with two and a quarter inches or more in D. b. bicornis, and by the fact that the occipital crest is much less elevated than in the larger animal. I may say that I personally believe that it is difficult, if not impossible, to divide the two races at any particular point and that if sufficient material were available it would be apparent that the divergence of the two is gradual and progressive.

Dentition

The teeth are peculiar, there being no incisors or canines in either jaw. There are seven "cheek" teeth, four premolars and three molars; the first premolar is often missing in older animals especially in the lower jaw. The teeth consist of dentine and enamel only, no cement being present. The outer surfaces of the teeth remain smooth, but the inner surfaces develop deep ridges and

Reproduction

The gestation period is 540 days (International Zoo Year Book 1959). One calf is produced, twins being unknown. The adult female possesses two mammae situated in the inguinal region, and the young suckle up to at least two years of age. The period of growth from birth to maturity, which is normally quoted as five years, is probably about seven, although I am informed that an animal at present in the London Zoo is nine years old and is still growing. Young rhino are lighter in colour than the adults. What period elapses after the birth of a calf before the cow again comes in season I am uncertain, but I think it is probably from eight to ten months.

Longevity

There are, so far as I can find, no figures on which one can base an estimate, even an intelligent guess, as to a rhino's longevity. There is a record of one living in captivity for over 20 years, but there is no reason to

suppose that they might not live to twice that age or even more, either in captivity or in the wild state. Incidentally a rhino in captivity is not difficult to tame even if captured full grown, while a very young one becomes much attached to the person who feeds it in a few hours.

Навітат

Rhinos are found in a wide variety of habitats; forest, bush, plain and desert. They thrive in the high rain-forests and cloudsoaked moorlands of the great mountain ranges. They are equally at home in sunbaked, lava-strewn sandy wastes. Almost any of the intermediate types of habitat appear to suit them, with one exception: they are not found in areas that have a hot humid atmosphere.

DAILY ACTIVITY

Whatever his environment, the routine of a rhino is more or less the same. The event of outstanding importance is the daily drink, and this is normally taken soon after sundown. In some places where rhino are completely immune from molestation they drink regularly during the afternoon. usually between 3 and 4 o'clock, but the vast majority water at night, sometimes staying in the vicinity of a waterhole for hours on end. While there they are often in playful mood, and indulge in gargantuan romps and gambols to the accompaniment of squeals and snorts. While drinking they often take the opportunity to have a good mud wallow. I have also seen them, like any sparrow, having a dust bath in volcanic ash, but they far prefer mud. They get themselves well plastered, and then indulge in massage by rubbing against stones or trees, which in turn become plastered. It is incidentally by no means uncommon for them to get stuck in mud, and I have known of several instances where animals have thus died of exhaustion and starvation.

They seem to prefer stagnant water, and will choose a mud puddle in preference to a clear stream. If a water hole is drying out they will dig, using their forefeet like a dog, and Percival, my predecessor as Game Warden of Kenya, records seeing holes in a dry river bed a metre deep dug by rhino. In desert country, where rhino are sometimes found 30 miles or more from water, it is doubtless the case that they may drink only on alternate nights, or even less frequently,

getting moisture from various succulents, euphorbias of which they are very fond, Adenia, aloes and other plants. But where possible they water once in each 24 hours.

The normal gait of an undisturbed rhino is a fast walk in which the two legs on the same side move together, but it is noteworthy that when going to water he shows a sense of urgency and trots for considerable distances, his action being similar to that of a high-stepping horse. Returning from water to his feeding area, usually from 5 to 15 miles away, using the same well-worn path by which he came, for he is a most conservative creature, he adopts a more discreet pace. At first he probably does not feed, but further on will snatch a mouthful here and there as he goes. Serious feeding does not commence till he gets to his "home" ground where he browses on shrubs and trees, particularly acacias; he is often seen on the plains, apparently eating grass, but in fact he is almost certainly eating the stunted scrubby plants, and woody herbs, which thrive in the coarse grass. At about 9 a.m. he looks for some shade in which to pass the heat of the day, and there he normally remains till about 4 p.m., or earlier on a cloudy day; then he begins to feed once more until it is time to set out again towards water.

The resting period is spent for the most part asleep, sometimes flat on his side but more usually asleep with the legs doubled under the body, or standing up with the head down in the attitude of utter dejection which is his most characteristic pose. While asleep he relies for warning of danger largely on his attendant tick birds (Buphagus), which keep watch over him at all times and alert him when necessary by flying off with noisy demonstrations. It is a comical sight to see a rhino thus rudely awakened jerking quickly from side to side with ears stuck forward seeking to locate the trouble, until the tick birds again return to perch on his back and give him the "all clear."

I mentioned above "well worn paths." These rhino paths are a very familiar feature of any area inhabited by rhino. They are some 20 inches wide, having room for each set of foot-prints side by side. Percival, in his book A Game Ranger's Note-Book (1924), makes an interesting point when speaking of the value of these paths in unknown country as showing the way to water. He points out, however, that it is necessary to distinguish between them and native-made paths; the native track on coming to a thorn were together for some days; it consisted of an tree goes well round it, while a rhino path brushes or goes under it. Rhino paths, either to water or round and about the feeding area are not fitted to the contours, and well graded, as are elephant paths. In fact they very often rise steeply and in broken country there is a path running along the ridge, and over the highest point, of every hill.

SANITATION

Frequent features beside every rhino path are "scrapes," the places where the animals drop their dung. In areas where rhino are numerous, especially near water, a "scrape" may be ten or more yards across, every animal that passes apparently adding his contribution. The dung in these "scrapes" is always broken up and scattered. The animal works his hind legs backwards and forwards while actually dropping his dung and also kicks it about with his hind legs when he has finished. The native explanation of this curious habit is that it is in accordance with orders issued by elephant, which dislike seeing dung looking so like their own lying around. Knowing the respect that rhino normally have for elephant, I can think of no better explanation!

While on this subject I may add that a rhino does not urinate at the same time that he drops his dung as, for example, elephants often do. When he does so, it is a lengthy business, the male directing backwards between his hind legs a powerful jet, whereas the female ejects spasmodic bursts of spray. In the area occupied by D. b. somaliensis certain stones are used by the rhino for urination, as dogs use a favourite lamp post, and these stones become coated with a thick white concrete-like deposit. So far as I know. this habit is peculiar to the desert-dwelling race.

GROUP STRUCTURE

Rhino are usually met with singly, or in pairs or threes. A pair is a female and calf, or a male and female; a party of three is usually a cow with one well-grown and one small calf; a solitary animal is most probably a male or a nearly full-grown calf which has just left its mother. A cow is never accompanied by a bull when she has a very small calf. A calf always follows the mother, though with white rhino the calf leads. Very occasionally a party of four or more are seen, and I remember once a party of five which

old bull and a younger bull, two cows and a nearly adult calf.

MATING

Mating takes place at any time of year. Hunter has recorded that in one bush area which held a large rhino population a great preponderance of females came in season at one particular period—between September and November—but this conformity is unusual. The acts of mating may be repeated at intervals over several days and are protracted affairs; each occasion lasts for an hour or more, much time being lost in the preliminary sparring for position, which includes the bull placing his front feet on the back of the neck of the cow. Mating is almost always preceded, and usually succeeded, by violent attacks on the bull by the

The mating of a cow is probably confined to one bull in a season, though the converse is not the case and Cowie, Director of the Royal National Parks of Kenya, has told me that he once saw a bull serve two cows in quick succession, the bull receiving the usual attack from the first cow in the brief interval. Fights between bulls when a cow is coming into season are frequent, but there is some reason to suppose that once mating has taken place the successful suitor is not again challenged. At other times they do not fight, although I have heard of females fighting among themselves. At normal times two rhino on meeting regard each other at first with suspicion, then incipient defiance and potential resentment, but these soon pass and leave the tolerance of indifference.

Vocabulary

Rhino make a variety of noises. The one most commonly heard is the terrific puffing snort, repeated three or four times, given when the animal is frightened or angry and particularly at the beginning of a charge. They also growl and grunt when fighting, and squeal when mating or playing or when angry. Two less common noises may be mentioned, one a ghastly shrill scream sometimes made with the animal's expiring breath, and never repeated; the other I have never heard, but it has been described to me by a very reliable observer, Adamson, the Game Warden in charge of the northern part of Kenya. Adamson says he has heard it only when an animal is approaching a water



Adult male showing sores behind the shoulder and on the back.



Adult female and calf (probably 2-2½ years old)

hole, and he thinks that it is evoked by pleasurable anticipation. He imitated the noise for me. I can only describe it as being like a man trying to get his breath after receiving a violent blow on the solar plexus. It may also be a mating call but on that point I am uncertain. It may be worth recording that a rhino may be called from a considerable distance by a person who makes a noise imitating the puffs and snorts of the alarm signal.

LOCOMOTION

One of the most astonishing things about rhino is their quite extraordinary agility in relation to their bulk. They can get off the mark like any Olympic sprinter; they can turn on a sixpence, and make a polo pony look a clumsy cob. Over a short burst they can, I believe, reach nearly 30 miles an hour. Their normal gait when frightened is a trot, with head up and the tail held at first over the back and later horizontally and they may keep this up for miles, with an occasional short halt to listen. They gallop only when charging or wounded or seriously alarmed; it is incidentally characteristic of them when hit by a bullet to spin round and round before falling or dashing off on a last frantic rush. In a charge the head is lowered and the tail down. When making a turn at speed they remind one of a cat cornering a building with a dog after it, for their legs are splayed outwards, and they are in very truth "ventre-aterre." It is worth remarking that a rhino can get along quite well on three legs, while an elephant in similar circumstances is completely anchored.

DISPOSITION

The speed of which a rhino is capable brings us to one of the most discussed of all questions that concern Africa and its fauna. What is, in fact, the real disposition of the black rhino? Is he a malicious monster, eager to attack every human being he meets, or is his charge merely a hasty and ill-considered attempt to get away, at all costs, from danger?

I think that, after more than 30 years of experience, I have gained some conception of the answer. In order to simplify the explanation of my ideas I will divide rhino very approximately into three groups according to temperament, as follows:

(a) contains rhino in areas where they have for many years been hunted by

natives using poisoned arrows. Such areas are often densely covered by thorn bush or scrub.

(b) contains rhino which dwell in open plains or areas sparsely covered with bush, and peopled by pastoral tribes.

(c) includes all other rhino; those in fact which have not been particularly conditioned by contact with mankind as have the animals in groups (a) and (b).

(a) and (b) I can deal with most easily by considering two contiguous areas in Kenya. For (a) I will take the Ngulia Hills. Here rhino have been hunted from time immemorial by the Wakamba with their light, poison-tipped arrows. The result is a race of truculent animals ready to charge instantly, for in offensive action lies the secret of their survival. An animal running away would have an arrow flicked into his stern and certain death would ensue. A charging animal sends the hunter frantically diving for his life through thorn bush, and gives no chance whatever of using the bow. So the Ngulia rhino exemplify the virtue of the French dictum, "Toujours l'attaque."

For (b) we will take the nearby plains of the Masai Reserve. Here the pastoral Masai, with their vast herds of cattle, share the country with the rhino and many other game animals, in a "live and let live" atmosphere of mutual tolerance that is almost Arcadian. The Masai leave the rhino undisturbed unless, as rarely happens, some individual beast, in a fit of temper or arrogance, charges their cattle or attacks the women at a water hole, when he is promptly speared. A race of peaceable well-behaved animals has thus grown up, always ready to retire unless provoked beyond endurance, and here another French dictum is surely appropriate: "Toujours la politesse!"

I have now mentioned two extreme types of rhino. What about the host of intermediates in class (c)? To state an obvious truism one can only say that their actions will depend on the individual beast and the many and various attendant circumstances. I need not enlarge on "the individual beast." Some are moderately even-tempered, and some irritable, some brave and some timid; some volatile and some phlegmatic. All one can say is that the individual temperament of a rhino will at any moment play a part in deciding his action. Various conditions make for trouble, while certain others

very small calf will seldom charge home; she will shear off unless you are very close to her. Rhino have an acute sense of smell which incidentally functions even when the beast is asleep. Their hearing is also good but their sight is extremely poor and they are said to be myopic; objects, unless at a few yards range, have a blurred outline. I am sure that many charges commence as curiosity, which leads animals to come closer to identify a moving object, and end up as a deliberate attack when they find themselves so close that they fear to retreat. I am clear on one point. Other things being equal, if a rhino sees you first he is most likely to charge; if he hears you first he is least likely to charge; if he smells you first ...? To conclude this psychological survey. I believe that the great majority of the rhino in group (c) do not wish to press home a charge, unless their own stupidity or short sight gets them too involved to withdraw. A shout, or a shot into the ground in front, will often turn a charge however determined it appears. It is perhaps significant that a rhino which has charged and missed will very seldom return to hunt for his objective.

RELATIONS WITH OTHER SPECIES

Rhino seem to concern themselves little about the other game among which they live, with one exception; they have a healthy respect for elephant and will almost always give way to them, except sometimes at a water hole when they may successfully contest the issue. They do not appear to mind an old bull elephant but are genuinely frightened of cows, which is not surprising as I have personally known of a number of cases of rhino, particularly cows with young calves, being killed by them, the calf sharing its mother's fate. Incidentally, elephant after killing a rhino will almost invariably cover the victim with branches and bushes. Other animals do not appear to interfere with rhino to any great extent, though a young one is sometimes killed by lion and I heard recently of an old bull being killed by two lions. On the other hand I once saw two rhino drive three lionesses off an ostrich which they were eating. The lionesses backed away as the rhino came up to the

reduce the risk. For instance a cow with a very small calf will seldom charge home; she will, and the rhino drove them some 200 yards before leaving them.

I know of one instance only of apparent friendship—or perhaps one should say permanent association—with other animals. It concerned two rhino and a large herd of buffalo; over a long period the daily resting period was taken by the rhino asleep in a forest glade surrounded by the buffalo and lying cheek by jowl with them.

SORES

A peculiarity of rhino that gives rise to much speculation is the prevalence on them of open sores. These vary in size from one or two to six inches across and are found low on the sides and front of the body. There is almost invariably one at the base of the neck and another behind the shoulder. Various suggestions have been made about their origin; that they are caused by fights, or by wounds from running against fallen trees; that they are glandular; that the tick birds, which are known to exacerbate small sores made by ticks, are responsible. I am personally uncertain, but I think it probable that the majority of them originate as a result of constantly rubbing against a stone or a tree in an attempt to dislodge ticks. Rhino are always infested with ticks which often settle in a very sensitive spot. A factor that undoubtedly tends to make any sore on a rhino chronic is the fact that the animal's skin, thick as it is, has an extremely poor blood supply; healing is thus a very slow process. I may add that, during periods of courtship, these sores appear to exercise a strong element of fetishism.1

RHINOCEROS HORN

The horn of a rhino is not of course a true horn at all, but "a compact hard mass of agglutinated hair-like fibres which are an outgrowth of the skin." There are normally two horns, though I have twice seen an animal with three and heard of others. "The horns rest on the nasal bones, where they are held by their continuity with the thick skin of the snout." Horns vary greatly in size and shape, but in several particulars they are fairly constant. The following generalisation takes no account of freak horns. The anterior horn, which is nearly always longer, has a backward curve,

the degree of curvature varying from an almost straight line to a semicircle. It is rounded in section, and has a rounded base. wherein it differs from that of the white rhino which is square in front. The posterior horn also has a rounded base, but it is laterally flattened and shaped like a broad dagger. The horns differ considerably between the sexes, the anterior horn of the male being much more solid and tapering from the base gradually, whereas in the female there is a similarly heavy base, but from it emerges a much more slender and rapierlike horn. All horns are somewhat concave at the base, such concavity appearing to act in part as a suction cup in relation to the bone on which the horns sit. The longest horns known to me come from the high forests of Mount Kenya, the Aberdare range, and the northern foothills of Mount Kilimaniaro. The record horn, $53\frac{1}{2}$ inches, was I think obtained in the latter area and in these three zones I have, over the years, seen some half-dozen animals whose horn was in the region of 40 inches at least. The thorn-bush country at lower altitudes and the northern deserts breed short stubby horns, anything over 20 inches being exceptional in those areas.

The Kenya Game Department possesses several magnificent pairs of horns and also has a number of unusual specimens. The gem of the collection is undoubtedly a horn some three and a half inches long and two inches wide, which was grown on the side of a rhino's rump about 12 inches from the root of the tail. There are two other smaller horns from another animal which were growing from the skin on its flank. There is also a magnificent specimen of what I am confident is a secondary horn. The first horn had undoubtedly been wrenched or knocked off, and a new horn had in course of time developed, perfectly cylindrical in shape and quite flat on top.

A rhino does not use his horn for digging for roots, etc., as an elephant does his tusks, but he uses it frequently to loosen earth or soft rock where there is a salt lick. Adamson has described to me an astonishing cave excavated in the base of a 20-foot cliff on the side of a donga on Marsabit Mountain. The cave is some ten yards deep and ten wide and about six and a half feet high. The sides, and also the roof, are scored with innumerable furrows like the marks of countless pickaxes. I have seen the same

kind of thing on a much smaller scale in many other places where there are mineralised deposits, for rhino are extremely fond of the latter and constantly visit them.

Rhino horn is a very valuable commodity; indeed, with the exception of ambergris and various furs, it is perhaps the most highly-priced animal product in the world. Its value, about £3 a pound locally at present, results from the demand for it in Asia, where in India and China and elsewhere it is believed to have powerful aphrodisiacal properties. I cannot say whether such claims for it are well founded, or whether they are based on symbolism and auto-suggestion.

POACHING

The value of rhino horn makes it inevitable that the animals will be killed by poachers. In Kenya by far the greatest toll is taken by the hunting tribes which use poisoned arrows, and among them the Wakamba are the principal offenders. The poison. a black treacly substance, is made by boiling down a decoction of the branches of a tree that looks very like a wild olive and is called Acokanthera schimperi Schweinf. When fresh the poison is very virulent. but its power wanes rapidly when exposed to the air, and a poacher keeps a thin tape of skin wound round the poison on his arrow until he is about to take his shot. A rhino hit by an arrow with fresh poison, no matter where hit, will quickly succumb.

In the north-western parts of Kenya many rhino are killed with the aid of an ingenious leg snare attached to a heavy log. A twisted raw hide thong—usually made of giraffe hide—is formed into a noose, and this noose is laid in a rhino path above a support beneath which a hole is dug. The support is like a wheel with the spokes lying loose inwards towards where a hub would be. An animal puts his foot through the "wheel" which stays on his leg long enough to allow the noose lying on top of it to tighten. The wretched animal then drags round, perhaps for several days, a heavy log until he becomes exhausted. when he falls an easy prey to the spearmen who are following the unmistakeable spoor.

CONSERVATION

I must end on a serious note of warning. The Rhinoceros family have almost disappeared from Asia. No one who considers

¹ Editorial note: it is now well established that a filarial parasite, probably transmitted by a biting fly, is present in these sores. Not everyone who has studied the sores, however, agrees that the parasite is the primary cause of the sore as opposed to a secondary infection.

their distribution in Africa today as compared with a hundred years ago can have any doubt that here the same sad process goes on, and rapidly. It is not poaching or any deliberate killing by human beings that menaces their survival, for poaching can be kept within reasonable bounds, and legalised killing reduced by special licences and heavy fees. The real threat to their survival lies within themselves. They spent still young and now, their adaptability

gone, they appear to be unable to extend their range into fresh areas. In these circumstances they will only survive in sanctuaries and reserves where their interests are absolutely paramount. In my belief there is no animal in the world today so greatly in need of skilled and sympathetic care and conservation. We must not neglect nor unduly delay the provision of such treatment. If we do we shall be too late; their evolutional urge while mankind was and nature will not forget, nor posterity forgive, our dereliction.

(Received for publication April 1963)

ECOLOGICAL SEPARATION OF THE LARGE MAMMAL SPECIES IN THE TARANGIRE GAME RESERVE, TANGANYIKA¹

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SUMMARY

The ecological separation of 14 common ungulate species living in close contact with each other in a Tanganyika game reserve is shown to be achieved by six different factors:

- 1. the occupation of different vegetation types and broad habitats;
- 2. the selection of different types of food;
- 3. the occupation of different areas at the same season;
- 4. the occupation of the same area at different seasons:
- 5. the use of different feeding levels in the vegetation;
- 6. the occupation of different dry season refuges in the Masai area when the competition for food is greatest (zebra and wildebeest).

Habitat preferences are indicated by the frequency distribution of each species along the central of three 8,000 yard parallel transect paths which were traversed nearly daily for four years. Characteristic patterns of frequency are apparent for each of the species in the vegetation zones represented in the transect area. Certain species show a tendency, sometimes strong, to concentrate along the boundaries between adjoining vegetation zones and in the ecotones between the zones. This is ascribed to a greater diversity of food, availability of shelter from the sun and/or greater protection from predators.

Records of the animal species eating particular plant species are shown and (qualified in the light of other observations) used to deduce food preferences. The species are classified broadly into grass-eaters, browsers and mixed feeders (grass and browse). In the case of the three common grass-eaters, buffalo, wildebeest and zebra, a percentage analysis of the grass species eaten indicates that little differential preference is shown but that they take the palatable grasses largely in proportion to the frequency in which they occur in the habitats most used by the ungulate concerned. Buffalo are

separated by their preference for denser vegetation. Wildebeest and zebra largely overlap ecologically in all respects except that the bulk of the populations of each species move to different dry season areas. Those species which are able to live without drinking free water, notably impala and Grant's gazelle, are able to make use of wild areas of waterless country when the animals requiring water are forced to move into dry season concentration areas near water.

The influence of the animals on the habitats and on other species is discussed and instances are given of species helping to shape the habitat to the advantage of both themselves and other species. Elephants are the main habitat modifiers and their capacity to improve water supplies and change the vegetation, and their facilitation of the feeding of other species is described. The formation of mixed herds is interpreted as being protective to one or both species concerned and is a further important facilitation. Little or no hindrance of one ungulate species by another was seen although herbivores show antagonistic behaviour towards carnivores smaller than themselves.

Introduction

In the Tarangire Game Reserve fourteen ungulate species (excluding six very uncommon ones) live together in close proximity at a time when the food resources and sometimes the water supplies are critically low. The Reserve, which is described elsewhere (Lamprey, 1963), lies in the Acacia savanna of northern Tanganyika. The density of animals in the dry season concentration areas of the Tarangire is very high (Lamprey, 1961, 1963), nevertheless there is little, if any, evidence of overstocking and the consequent deterioration of land as there is in the neighbouring cattle areas of the Masai Steppe. Competition between the species for the limited food resources would be expected to occur but this would be alleviated by their ecological separation. The purpose of this

¹ Based on a chapter of a thesis accepted by the University of Oxford for the degree of D. Phil.